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Salmonine Introductions to the Laurentian Great Lakes:

An Historical Review and Evaluation of Ecological Effects

Stephen S. Crawford

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Salmonine Introductions to the Laurentian Great Lakes:

An Historical Review and Evaluation of Ecological Effects

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An Historical Review and Evaluation of Ecological Effects

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Abstract

This publication provides an historical review and evaluation of documented ecological effects associated with salmonine introductions to the Laurentian Great Lakes. The introduction of salmonines to the Great Lakes date back to the 1870s, when natural populations of native salmonines in the Great Lakes (e.g., lake charr, brook charr, Atlantic salmon in Lake Ontario) were in severe decline. Using newly developed hatchery technology, American and Canadian agencies released several non-native salmonines into the Great Lakes during the early era (1870–1960) of introductions. With the exception of brown trout and rainbow trout in some tributaries, the early introductions failed to establish self-sustaining populations.

Beginning in the mid-1960s, American and Canadian fisheries agencies began another intensive round of salmonine introductions to the Great Lakes that included brown trout, rainbow trout, chinook salmon, coho salmon and kokanee. The original objectives for these introductions were (1) to develop self-sustaining, wild-reproducing populations to exert biological control of nuisance alewife and rainbow smelt and/or (2) to develop new recreational fisheries. Chinook and coho salmon especially thrived on the abundant forage base in the open waters of the Great Lakes, and triggered a dramatic eruption of recreational salmon fishing. Since the 1960s introductions of salmonines to the Great Lakes increased dramatically, with estimates of total stocking in excess of 745 million fish for the period 1966–1998, an average of more than 61,000 non-native fish released every day for 33 years.

In many cases, populations of introduced salmonines were heavily stocked beyond levels of reproduction observed in the wild, primarily to support the put-grow-and-take recreational fisheries. One of the most dramatic effects that introductions have had on the non-native salmonines is the alteration of their life-history characteristics, including body form and function, feeding and spawning behaviour. Over time, fisheries managers changed their perception of alewife/rainbow smelt from a nuisance to an important prey resource that must be protected to support the recreational salmon fishery.

A review of scientific literature and technical reports from the past four decades was undertaken to evaluate the ecological effects of introduced salmonines on the Great Lakes ecosystem. Using established evaluation protocols, it was determined that there is evidence of significant ecological effects in six different categories: (1) diseases and parasites, (2) predation on native species, (3) competition for limiting resources, (4) genetic alteration, (5) environmental alteration and (6) community alteration. Taken together, this body of evidence supports the conclusion that the ongoing introduction of non-native salmonines poses an ecologically-significant risk to the Great Lakes ecosystem and its native organisms, and that the introductions should be terminated.

Résumé

Dans la présente publication, nous brossons un tableau historique et critique des répercussions écologiques prouvées de l'introduction de salmoninés dans la région laurentienne des Grands Lacs. Les salmoninés ont commencé à être introduits dans les eaux des Grands Lacs au cours des années 1870, lorsqu'on y a noté un grave appauvrissement des salmoninés indigènes (soit la truite grise, la truite saumonée et le saumon de l'Atlantique dans le lac Ontario). Ayant recours aux technologies avancées d'alors, les organismes américains et canadiens ont libéré plusieurs espèces étrangères de salmoninés dans les Grands Lacs pendant la période de 1870 à 1960. Si ce n'est de la truite de mer et de la truite arc-en-ciel, espèces qui sont arrivées à s'établir dans certains affluents, ces premières introductions n'ont pas réussi à produire des populations viables à long terme.

Au début des années 1960, les organismes américains et canadiens chargés des pêches ont lancé une autre phase intensive d'introduction de salmoninés dans les Grands Lacs. Les espèces visées comprenaient la truite de mer, la truite arc-en-ciel, le saumon quinnat, le saumon coho et le saumon kokani. Les objectifs de ces introductions étaient (1) d'établir des populations viables et aptes à la reproduction afin de faire la lutte biologique au gaspereau et à l'éperlan, estimés nuisibles, et (2) d'ouvrir de nouvelles possibilités en matière de pêche. Le saumon quinnat et le saumon coho se sont particulièrement bien établis en raison de l'abondance de poissons proies dans les eaux des Grands Lacs, ce qui s'est traduit par une véritable explosion de la pêche sportive du saumon. Depuis lors, les introductions de salmoninés dans les Grands Lacs ont considérablement augmenté et on estime que, pendant la période de 1966 à 1998, on a déversé plus de 745 millions de poissons dans les eaux des Grands Lacs, ce qui équivaut à une introduction quotidienne moyenne de plus de 61 000 poissons étrangers.

Dans nombre de cas, la densité des populations de salmoninés introduits était de beaucoup supérieure à ce qu'aurait permis la reproduction naturelle, ceci afin de soutenir la pêche sportive. Un des effets les plus significatifs de ces massives introductions sur les salmoninés étrangers est l'altération de leurs caractéristiques de cycle de vie, y compris la forme et les fonctions de leur corps, leur alimentation et leurs comportements de frai. Au fil des années les gestionnaires des pêches ont changé leur fusil d'épaule en déclarant que le gaspereau et l'éperlan n'étaient plus des espèces nuisibles, mais plutôt des espèces proies devant être protégées afin d'assurer l'avenir de la pêche sportive du saumon.

Nous avons réalisé un examen de la documentation scientifique et des rapports techniques publiés au cours des quarante dernières années afin d'évaluer les répercussions écologiques de l'introduction de salmoninés étrangers sur l'écosystème des Grands Lacs. Guidés par des protocoles d'évaluation reconnus, nous avons constaté des répercussions écologiques significatives dans six catégories : (1) les maladies et les parasites, (2) la prédation des espèces indigènes, (3) la rivalité découlant des ressources limitées, (4) l'altération génétique, (5) l'altération environnementale et (6) l'altération des communautés. Ensemble, ces constatations appuient la conclusion que l'introduction constante de salmoninés étrangers constitue une sérieuse menace écologique pour l'écosystème des Grands Lacs et pour ses organismes indigènes et que ces introductions doivent cesser.

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Special thanks to all of the researchers, librarians and archivists who assisted in my year-long search for background information and an original copy of the Burland-Desbarat photolithograph of Wilmot's pioneering Newcastle fish-breeding establishment; Prof. Hugh MacCrimmon (University of Guelph, retired) and wife Irene MacCrimmon, Diana Grandfield (great granddaughter of Wilmot), Helen Schmid (Clarke Township historian), Andrew Rogers (Canadian National Archives), Denis LaSalle (DFO Ottawa), Laurie Collins (DFO Bedford), Jeff Hawker and Gordon Miller (DFO Nanaimo) and to Dr. Don Noakes (DFO Nanaimo) for special dispensation and transportation of the original report.

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Executive Summary

The goal of this monograph is to provide an historical review and evaluation of documented ecological effects associated with salmonine introductions to the Laurentian Great Lakes. To date, no comprehensive reviews or evaluations have been conducted by any of the Great Lakes fisheries management agencies that participate in, or support, ongoing salmonine introductions. The absence of such a review is noteworthy, especially in light of evidence from the scientific literature that salmonine introductions have had significantly-negative ecological effects on the native members of the Great Lakes community.

History of salmonine introductions

The introduction of salmonines to the Great Lakes dates back to the 1870s, when natural populations of native salmonines in the Great Lakes (e.g., lake charr, brook charr, Atlantic salmon in Lake Ontario) were in severe decline. These declines were largely attributed to human activities, especially habitat degradation (urbanization, damming, deforestation, agriculture) and overharvesting. Early salmonine introductions in the Great Lakes began with the development of hatchery technology, like the Newcastle facility constructed by Samuel Wilmot for rehabilitation and support of native Atlantic salmon in Lake Ontario.

Several non-native salmonines were released by both American and Canadian agencies into the Great Lakes during the early (1870–1960) era of introductions:

Atlantic salmonines:	Atlantic salmon (*Salmo salar*), outside of Lake Ontario Brown trout (*Salmo trutta*)
Pacific salmonines:	Chinook salmon (*Oncorhynchus tshawytscha*) Coho salmon (*Oncorhynchus kisutch*) Rainbow trout (*Oncorhynchus mykiss*) Kokanee (*Oncorhynchus nerka*) Cutthroat trout (*Oncorhynchus clarkii*) Masu salmon (*Oncorhynchus masou*) Pink salmon (*Oncorhynchus gorbuscha*)
Arctic salmonines:	Arctic charr (*Salvelinus alpinus*)

These early salmonine introductions were intended to develop self-sustaining, wild-reproducing populations to support food, commercial or recreational fisheries. With the exception of brown trout and rainbow trout populations in some Great Lakes tributaries, the early introductions failed to achieve their objectives. Pink salmon, a non-native Pacific salmonine unofficially released to Lake Superior in 1956, quickly established self-sustaining, wild-reproducing populations in the Great Lakes.

Beginning in the mid-1960s, American and Canadian fisheries agencies began an intensive round of salmonine introductions to the Great Lakes that included brown trout, rainbow trout, chinook salmon, coho salmon and kokanee. The objectives for these introductions were (1) to develop self-sustaining, wild-reproducing populations to exert biological control of non-native planktivorous fishes, and/or (2) to develop new recreational fisheries. Alewife and rainbow smelt had become abundant in the Great Lakes, and in some cases were considered to be an aesthetic, economic and ecological nuisance. Both alewife and rainbow smelt had been introduced by humans to the Great Lakes; alewife were released unintentionally, and rainbow smelt were released intentionally as food for introduced Atlantic salmon.

Recently, continued declines in the abundance of alewife in Lake Michigan and Lake Ontario have raised arguments about whether to decrease stocking of salmonines and prevent a collapse in the alewife populations, or to maintain/increase stocking and support the expanding recreational fisheries. In either case, it has become clear that biological control of alewife and rainbow smelt is no longer a major objective for fisheries managers. Ironically, the alewife and rainbow smelt that were originally considered a novelty, then a nuisance, are now considered by sportsmen and fisheries managers to be a valuable food resource for introduced salmonines. Currently, the only major objective for salmonine introductions in the Great Lakes is the development and maintenance of recreational fisheries.

Despite explicit ecological warnings made in the 1960s about the potential for ecological damage resulting from salmonine introductions, American and Canadian fisheries agencies continued with their Great Lakes salmonine introduction programs. Neither American nor Canadian fisheries agencies conducted comprehensive pre- or post-introduction ecological evaluations of salmonine introductions. Since the 1960s introductions of salmonines to the Great Lakes have increased dramatically, with estimates of total stocking in excess of 745 million fish released during the period 1966–1998, an average of more than 61,000 fish released every day for 33 years. The vast majority (i.e., >91%) of these introduced salmonines have been released by American hatcheries.

Effects of introductions on the introduced salmonines

Introduced salmonines have generally survived and grown well in the Great Lakes ecosystem, especially when feeding on forage fishes such as alewife and rainbow smelt. Recently, concerns have been expressed about the decline observed in growth and survival rates of introduced salmonines in the Great Lakes basin, especially chinook salmon. It has been hypothesized that stocking of the introduced salmonines has led to reductions in the availability of their forage base, especially alewife. Introduced salmonines have developed a reputation for dispersion and migration, especially in the open-lake environments of the Great Lakes basin. These movements have been described at the intra- and inter-basin level, and have been associated with colonisation of habitat where the fish had not previously been stocked.

There is a high degree of uncertainty regarding reproduction of the introduced salmonines in the Great Lakes. For species such as brown trout and rainbow trout, reproduction can reach levels that support wild populations, especially in cases where the population is stream-resident. However, for pelagic species such as chinook and coho salmon, the ability to maintain populations through wild reproduction is highly suspect. Some researchers have argued that the quantity and quality of spawning habitat in Great Lakes tributaries are limiting factors for reproduction. In many cases, populations of introduced salmonines are thought to be heavily stocked beyond levels of reproduction observed in the wild, primarily to support the put-grow-and-take recreational fisheries.

One of the more alarming effects that introductions have had on the non-native salmonines is the alteration of life-history characteristics of the introduced species. Shifts from 'normal' patterns have been observed in body form and function, feeding and spawning behaviour. Such life-history shifts can be expected when organisms are transplanted to novel environments, and are subjected to novel ecological and evolutionary pressures.

Effects of introductions on the receiving Great Lakes ecosystem

Non-native diseases (e.g., furunculosis, whirling disease) and parasites (e.g., *Philonema oncorhynchi, Ergasilus nerkae*) may have been introduced to the Great Lakes along with the introduced salmonines. Of all the Great Lakes species, native salmonines (lake charr, brook charr) are likely the most susceptible to these introduced diseases and parasites. The intensive culture of hatchery-reared salmonines poses a threat to native fishes by artificially increasing the disease and parasite 'reservoir' that native fishes are exposed to in the wild.

Predation by introduced salmonines on native species in the Great Lakes basin is a serious concern because the stocked fish are '*generalist, vertebrate predators*' — they have the ability to feed on a wide variety of prey species. This danger is particularly evident in Great Lakes tributaries where juvenile and stream-resident salmonines forage on a common supply of native species, including a variety of invertebrates and fishes. In the open-lakes, many introduced salmonines forage primarily on alewife and rainbow smelt, however they also feed on native sculpins, bloater and yellow perch — at levels that may pose a significant threat to the supporting forage populations. It has been predicted that introduced salmonines will switch to alternate, native species as alewife populations decline and/or stocking for the recreational fisheries increases. This switch in behaviour can expose the populations of native forage species to the risk of excessive mortality, especially in situations where stocking programs exceed carrying capacity of the native community.

Competition between introduced salmonines and native species in the Great Lakes basin has been investigated by a limited number of experimental studies. In tributaries, there is evidence that the larger and more aggressive introduced salmonines outcompete smaller native species (e.g., brook charr) for limited food, cover and stream position. In open-lake environments, studies have shown that introduced salmonines forage voraciously on the same species that is dominant in lake charr diets (i.e., the declining alewife populations). Spatial bioenergetic models have shown that lake zones of growth potential for lake charr and chinook salmon have a high degree of overlap. There is also evidence of spawning-phase chinook salmon directly interfering with spawning lake charr in one of the last two self-sustaining populations in Lake Huron.

Genetic alteration of native species by introduced salmonines in the Great Lakes can be either direct or indirect. There is evidence of direct alteration effects, such as hybridization and introgression with native species. Indirect effects, like those associated with declines in population abundance of native species, have occurred as a result of intensive stocking of introduced salmonines.

Environmental alterations by introduced salmonines have been reported in both tributaries and open-lake environments of the Great Lakes basin. In tributaries, spawning salmonines dig up nests or superimpose their redds on the habitat of native species. These physical alterations have been shown to have community-level effects on the abundance and distribution of native fishes and invertebrates in the tributaries. Spawning runs of introduced salmonines have also been shown to transport significant levels of contaminants upriver from the lakes.

Community alteration occurs when the structure or function of a native community is affected by introduced species. In the Great Lakes basin, community structure has been affected by the feeding habits and competitive interactions of the introduced salmonines. In open-lake environments, introduced salmonines have taken on a dominant role as upper-level predators — yet they exist in numbers often more determined by hatchery production capacities than by the characteristics of the ecological community they live in. In Great Lakes tributaries, introduced salmonines have been shown to alter community ecology by increasing the levels of limiting nutrients and toxins picked up in the open-lake environments. A conspicuous example of this kind of community alteration occurs when introduced salmonines embark on massive, and typically lethal, spawning runs into the tributaries. The spawning runs of the introduced salmonines stand in contrast to the typical stream-resident or lake-resident tendencies of the native brook and lake charrs, respectively.

Taken together, this body of evidence supports the conclusion that the ongoing introduction of non-native salmonines poses an ecologically-significant risk to the Great Lakes ecosystem and its native organisms, and that the introductions should be terminated.

1

Introduction

There are few issues associated with Laurentian Great Lakes fisheries management that can stir up as much controversy as salmon. It seems everybody has a strong opinion on the topic, including recreational anglers, commercial fishermen, government fisheries managers, local business operators, politicians, academics, environmental protection groups and Aboriginal communities. But why does the controversy arise? In some cases, it may be a political contest over jurisdiction. In other cases, it may involve cultural or economic factors. However, in many cases the conflicts have to do with the ecology of stocking salmon in the Great Lakes.

One common characteristic of ecological arguments surrounding Great Lakes salmonine introductions is a lack of necessary information. This lack of information applies as much to historical events associated with the salmonine introductions, as it does to the ecological consequences. The information presented by proponents or opponents is often unreliable. For example, consider the following misconceptions regarding introduced salmonines in the Great Lakes:

> *"Anadromous rainbow trout were introduced approximately 100 yr ago to Lake Superior and have developed self-sustaining populations that support a highly prized sport fishery. Many anglers in the region consider rainbow trout a native and the more recently introduced chinook salmon as an exotic. In this case, the distinction between native and exotic species by society appears dependent on the time since introduction, with the transition from exotic to native measured, at most, in a few human generations rather than glacial epoches."* (Krueger and May 1991, p. 74)

> *"... second generation adult freshwater [coho] salmon have retained the fecundity characteristics of freshwater salmon reared from Pacific Ocean eggs, suggesting that coho salmon will become part of the indigenous fish fauna of the Great Lakes."* (Stauffer 1976, p. 1154)

Obviously, there is a great need for clarity when it comes to ecological issues associated with Great Lakes salmonine introductions.

1.1 Goal and objectives of this report

The goal of this report is to present an historical review and evaluation of documented ecological effects of salmonine introductions to the Great Lakes, in a comprehensive and understandable manner. To achieve this goal, three objectives have been established:

- Review the history of salmonine introductions to the Great Lakes,
- Review the ecology of salmonine introductions to the Great Lakes, and
- Evaluate the ecological effects of salmonine introductions to the Great Lakes.

I will be discussing these subjects primarily from an ecological perspective, rather than on the basis of social or economic values — factors which must also be considered when developing and employing an effective conservation ethic for fisheries management (Crawford and Morito 1997).

1.2 Sources of information

This review was first prepared as a report for the Chippewas of Nawash First Nation on the ecology and policy associated with introduced salmonines in the Great Lakes (Crawford 1997), and was first presented at the 1998 Canadian Conference for Fisheries Research in Kingston, Ontario. Since then, I have divided the report into two different manuscripts: this monograph — focussing on scientific aspects of the issue, and a companion editorial which will explore the social, economic and political opinions regarding the issue. This monograph is based largely on a comprehensive search of the primary and technical scientific literature published from the period 1966 to 2000. During this literature search, I kept detailed notes of historical references, reports and popular publications that provided additional details regarding the history and/or ecology of introduced salmonines in the Great Lakes. I have attempted to be as thorough as possible in my search, hoping that this review will serve as a useful reference tool for those who will come down this path in the future.

From an historical perspective, I found myself searching through archives to track down first-hand documentation, to the best of my ability. As indicated below in my apology to historians, there is still plenty of room for their professional analysis of this subject. One of the historical sources that served as a lightning rod for my research was an early report of Samuel Wilmot (1878) on the "*Several Fish-Breeding Establishments and Fish-Culture in Canada, during the season of 1877.*" This report not only documents the very inception of salmonine introductions in the Great Lakes, it does so in first-hand account by a titan of Canadian fisheries science. The exceptional photo-lithographs of Wilmot's pioneering fish-breeding establishment at Newcastle, Ontario are used here to give readers a graphic impression of how this whole story began.

The introduced salmonine stocking tables and graphs presented in this report have been compiled from files and updates gratefully received from the Great Lakes Fishery Commission and many of its member agencies (see Appendix I). To my knowledge, this is the first attempt to present comprehensive data for such stocking in the Great Lakes; data in a form that distinguishes species, lake, year and jurisdiction of origin. Prior to this review, researchers were forced to deal with subsets of data (e.g., Kocik and Jones 1999) or were at risk of misinterpreting incomplete datasets that were available through the Internet without the required caveats (e.g., FAO 1999). Having said this, it is important for the reader to interpret the stocking data I present in this review with caution. These data are general summaries of accounting, and they will surely be updated as efforts to reconstruct Great Lakes stocking history continue. The data do not identify the developmental state of release, an important factor to consider in evaluating ecological effects; however, this information was not available for most of the data received from the GLFC and associated fisheries agencies. The important point here is that I have tried to use broad strokes in portraying general trends in the stocking of introduced salmonines to the Great Lakes during the period 1966–1998. I hope that the reader finds these trends to be insightful, without exceeding the limitations of the available evidence.

Finally, I have included lively colour photographs of various introduced salmonines that currently support recreational fisheries in the Great Lakes drainage basin. These images are intended to set an historical counterpoint to the photolithographs of Wilmot's hatchery, and to provide a reminder of what these creatures really are — and their role in modern Great Lakes fisheries management. The photographer who contributed many of these images is an avid angler and is quite familiar with the issues.

1.3 Definition of terms

Descriptive terms in ecology (e.g., exotic, introduced, non-native), as in all scientific disciplines, carry implicit biases. Many of these terms are based on value judgements; judgements that may lead to variable meanings depending on who is using the term (Weir 1977; Nico and Fuller 1999). The point is that while such value judgements in terminology may not be avoidable, it is important to try and recognize them explicitly.

For the purposes of this report, I have adopted the American Fisheries Society's (AFS) "Recommended Standardized Terminology" associated with introduced organisms (Shafland and Lewis 1984; see also Kohler and Stanley 1984). Following this standardized terminology, the following definitions will hold in this report:

Introduced:

> *"A plant or animal moved from one place to another by man (i.e., an individual, group, or population of organisms that occur in a particular locale due to man's actions)."* (Shafland and Lewis 1984, p. 17)

This definition is also consistent with the United Nations' "*Precautionary Approach to Capture Fisheries and Species Introductions*" (FAO 1996, p. 7). Within the AFS classification scheme, there is a further division of 'introduced' organisms, based on their native geographic distribution:

Exotic:

> *"An organism introduced from a foreign country (i.e., one whose entire native range is outside the country where found)."* (Shafland and Lewis 1984, p. 17)

Transplanted:

> *"An organism moved outside its native range but within a country where it occurs naturally (i.e., one whose native range includes at least a portion of the country where found)."* (Shafland and Lewis 1984, p. 17)

Obviously, both of these terms are based on political, rather than ecological, considerations. Since the country of origin is largely irrelevant to an ecological review and evaluation, I will avoid using the terms 'exotic' and 'transplanted.' Instead, I will attempt to be consistent in my use of the term 'introduced' as defined above. It should be noted that the act of 'introducing' a non-native species is not restricted to the first occurrence, but includes all subsequent or ongoing releases (see Krueger and May 1991).

1.4 Native and introduced salmonines of the Great Lakes ecosystem

Ecologists often refer to the condition of the 'ecosystem' before and after an introduction. For the purposes of this report, I will use the term 'ecosystem' in its general sense as the combination of both the abiotic (non-living) components of an aquatic environment and the biotic (living) community of organisms that exist therein. With reference to the introduction of salmonines to the Great Lakes, this term should be taken to mean the entire drainage basin (cf. watershed, Hynes 1983): each of the five Laurentian Great Lakes (Superior, Michigan, Huron, Erie and Ontario), their connecting channels and all of the tributaries that drain into them.

From a taxonomic perspective (Table 1), the term 'salmonid' refers to all fishes belonging to the Family Salmonidae including the whitefishes (subfamily Coregoninae), the grayling (subfamily Thymallinae), and the 'trouts and salmons' (subfamily Salmoninae). The term 'salmonine' refers specifically to the subfamily Salmoninae, including the charrs[1] (genus *Salvelinus*), the Atlantic salmons (genus *Salmo*) and the Pacific salmons (genus *Oncorhynchus*). Recent investigation with nuclear and mitochondrial DNA (Domanico et al. 1997) has suggested that the North American Pacific salmonines can be divided into three subgroups of relatedness: (1) pink salmon (*O. gorbuscha*), chum salmon (*O. keta*) and sockeye salmon (*O. nerka*); (2) coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*); and (3) rainbow trout/steelhead (*O. mykiss*) as an outgroup.

Stearley and Smith (1993) clarified some common misconceptions regarding usage of English names within the Salmoninae:

> *"The terms "trout" and "salmon" do not refer to natural phylogenetic groups. These names originally referred to life history attributes: trout usually complete their life cycle in freshwater streams and lakes while salmon usually migrate to sea (according to English usage, but in Nineteenth Century French, the appellations signified the opposite; see Dumeril 1856). Interesting exceptions to common English usage include members of trout species that migrate to the sea — "salmon trouts" (sea-run* S. trutta*), coastal* O. clarki*, and steelhead (*O. mykiss*) — and members of salmon species that are lake-locked (kokanee, sebago, ouananiche, etc.). The common names based on these life history attributes need not match phyletic groupings. Both the Atlantic clade,* Salmo*, and the Pacific clade,* Oncorhynchus*, include trouts as well as salmons. The pacific salmon clade is a well-defined, cladistically advanced, monophyletic subgroup of six species, most of whose members die after spawning." (Stearley and Smith 1993, p. 26)*

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[1] In this report, fishes of the genus *Salvelinus* will be referred to as 'charr' as opposed to 'char.' This differs from the recommendations of the American Fisheries Society's *Common and scientific names of fishes from the United States and Canada* (Robins et al. 1991). Based on Morton (1980) and an important precedent of ongoing convention adopted by international experts of *Salvelinus* biology at four International Charr Symposiums held at Winnipeg (1980), Sapporo, Japan (1989), Trondheim, Norway (1994), and Trois-Rivières, Canada (2000), respectively, I use the spelling of the term 'charr,' as well as corrected conventions in the standard naming of 'brook charr' and 'lake charr.'

Table 1. Classification, origin, and status of salmonid species (family Salmonidae) historically or currently existing in the Great Lakes basin. Sources: Scott and Crossman (1973), Robins et al. (1991), Stearley (1992).

Family	Subfamily	Genus	Species	Common name	Origin
Salmonidae	Coregoninae	*Coregonus*	*artedi*	lake herring, cisco	Native
			clupeaformis	lake whitefish	Native
			hoyi	bloater	Native
			johannae	deepwater cisco	Native
			kiyi	kiyi	Native
			nigripinnis	blackfin cisco	Native
			reighardi	shortnose cisco	Native
			zenithicus	shortjaw cisco	Native
		Prosopium	*cylindraceum*	round whitefish	Native
	Thymallinae	*Thymallus*	*arcticus*	Arctic grayling	Native (extinct)
	Salmoninae	*Salvelinus*	*alpinus*	Arctic charr[a]	Arctic
			fontinalis	brook charr[a] = brook trout	Native
			namaycush	lake charr[a] = lake trout	Native
		Salmo	*trutta*	brown trout	Europe
			salar	Atlantic salmon	Native[b]
		Oncorhynchus	*clarki*	cutthroat trout	Pacific coast
			gorbuscha	pink salmon	Pacific coast
			keta	chum salmon	Pacific coast
			kisutch	coho salmon	Pacific coast
			masou	Masu salmon	Japan
			mykiss	rainbow trout, steelhead, skamania	Pacific coast
			nerka	sockeye salmon, kokanee	Pacific coast
			tshawytscha	chinook salmon	Pacific coast

[a] See footnote in text for explanation of the term "charr."

[b] Lake Ontario only.

Interestingly, this clarification of terminology foreshadows two very important concepts that will be discussed in this manuscript. First, the amazing diversity of life-history styles and evolutionary adaptation that can be found within the relatively small confines of the Subfamily Salmoninae. Second, the important difference between salmonines that typically exhibit repeat spawning (i.e., iteroparity) versus those that typically exhibit large-scale, one-time spawning runs followed by mass mortality (i.e., semelparity).

As indicated in Table 1, the only salmonine species which are native to the Great Lakes ecosystem are brook charr (*Salvelinus fontinalis*), lake charr (*Salvelinus namaycush*) and the Atlantic salmon that once existed in Lake Ontario. The existence of all other salmonines in the Great Lakes has resulted from human introductions.

For convenience of reading, the scientific names of all non-salmonid fishes mentioned in the text can be found in Table 2.

Table 2. Scientific and common names for non-salmonid fishes mentioned in the text. Source: Robins et al. (1991).

Family	Scientific name	Common name
Petromyzontidae	*Petromyzon marinus*	sea lamprey
Clupeidae	*Alosa pseudoharengus*	alewife
Osmeridae	*Osmerus mordax*	rainbow smelt
Esocidae	*Esox lucius*	northern pike
Cyprinidae	*Notropis atherinoides*	emerald shiner
	Notropis hudsonius	spottail shiner
	Pimephales notatus	bluntnose minnow
	Rhinichthys sp.	dace
	Semotilus atromaculatus	creek chub
	Semotilus corporalis	fallfish
Catostomidae	*Catostomus commersoni*	white sucker
	Hypentelium nigricans	northern hog sucker
Ictaluridae	*Ictalurus* sp.	catfish
Anguillidae	*Anguilla rostrata*	American eel
Gadidae	*Lota lota*	burbot
Gasterosteidae	*Gasterosteus aculeatus*	threespine stickleback
	Pungitius pungitius	ninespine stickleback
Percopsidae	*Percopsis omiscomaycus*	trout-perch
Centrarchidae	*Lepomis macrochirus*	bluegill
	Micropterus dolomieui	smallmouth bass
Percidae	*Perca flavescens*	yellow perch
	Stizostedion vitreum	walleye
	Etheostoma nigrum	johnny darter
Cottidae	*Cottus* sp.	sculpins
	Cottus cognatus	slimy sculpin

2

History of introduced salmonines in the Great Lakes[2]

The purpose of this section is to provide the reader with an historical context for salmonine introductions in the Great Lakes, in order to: (1) describe historical events presented in the scientific literature, (2) clarify persistent misconceptions regarding these events and (3) provide an historical context for understanding the rationale behind the salmonine introductions.

I am not presenting this work as an historian's evaluation or analysis of salmonine introductions to the Great Lakes — if such a treatise had already been written, I would have gratefully used it. Rather, this section is simply an accounting of information that became available to me as I worked my way through the scientific and technical literature. As such, there are certain specific issues that the reader should be aware of.

First, I have presented the historical narrative on a species-by-species basis rather than trying to spin a single, all-inclusive chronological tale. Although this approach may obscure some of the social and political forces involved in decision-making, it allows the reader to organize important dates and events in a comprehensible manner (Moyle 1997; Dill and Cordone 1997; Kocik and Jones 1999). Following the approach of Crossman (1968), Parsons (1973), McDowall (1978) and Nico and Fuller (1999), I have also adopted an operational distinction between 'early' (1870–1960) and 'recent' or 'modern' (1960–present) eras of salmonine introductions to the Great Lakes. Despite these efforts, some will argue that this historical review still does not effectively "capture the moods and understandings of the time." Hopefully, a professional historian will provide a comprehensive social evaluation of the Great Lakes salmonine introductions in the future.

Finally, the reader should be cautioned against the ever-present danger of anachronism in my accounting of history. There is always a tendency to judge the intentions or actions of people from a previous time in history, according to modern standards. This is neither appropriate, nor terribly useful. In this report, I have attempted to avoid such judgements.

2.1 Atlantic salmonines

2.1.1 Atlantic salmon (*Salmo salar*)

Atlantic salmon (Fig. 1) are native to the Great Lakes basin; however, their original distribution was restricted to the tributaries and open waters of Lake Ontario

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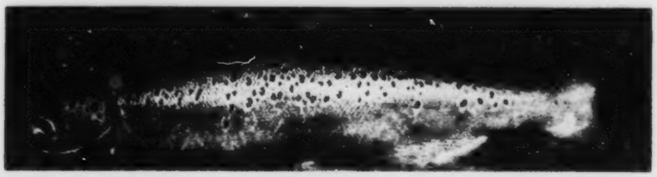
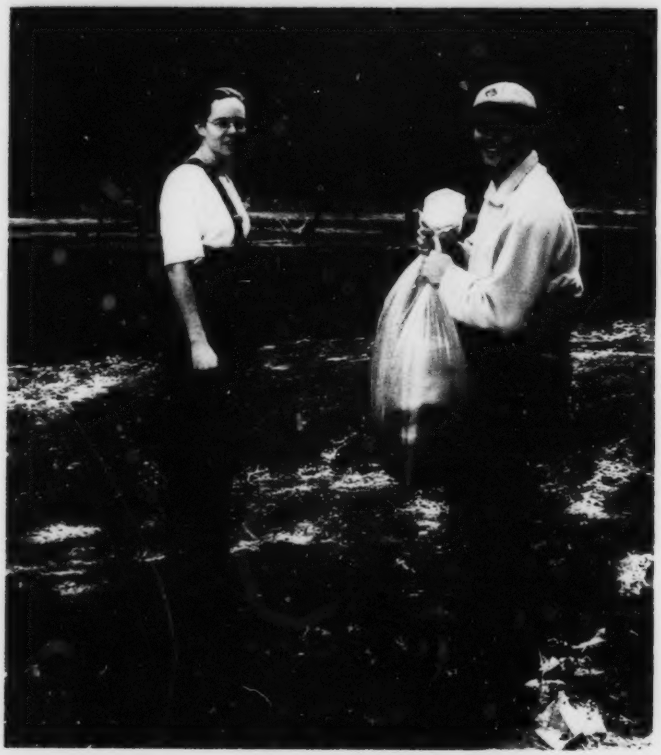
[2] I wish to recognize the contribution that certain researchers made by capturing and synthesizing the history of early salmonine introductions to the Great Lakes. Of particular note are the various works of MacKay (1969), Parsons (1973), Scott and Crossman (1973), MacCrimmon (1977) and Emery (1985). These authors provided a valuable base of information on the early history of Great Lakes fish introductions, and I have relied heavily upon them.

Fig. 1. Hatchery-reared Atlantic salmon (*Salmo salar*) being released to Orono Creek (Wilmot's Creek watershed, Lake Ontario basin) in October 2000. *Top photo*: 61.5 cm female Atlantic salmon just prior to release by research assistants Kelly Ramster (*left*) and Chris Weber (*right*). *Bottom photo*: Live transport of Atlantic salmon to fenced enclosures in Orono Creek. Atlantic salmon were native only to the Lake Ontario basin prior to extirpation by 1900; subsequently this species was introduced to the other Laurentian Great Lakes basins where they were not native. Atlantic salmon were the subject of the pioneering Newcastle hatchery fish-breeding program establish by Samuel Wilmot on this same tributary beginning in 1866. These photographs was taken as part of a research experiment conducted by Profs. Bill Beamish and David Noakes and Dr. Robert Scott (Axelrod Institute of Ichthyology, University of Guelph) in collaboration with the Ontario Ministry of Natural Resources. The general objective of research is to investigate the importance of factors that may prevent Atlantic salmon restoration in Lake Ontario and its tributaries — specifically the potential for competition between Atlantic salmon and introduced salmonines (i.e., chinook salmon, coho salmon, rainbow trout and brown trout). Photo credits: Steve Crawford.





(Scott and Crossman 1973). It is probable that the ancestors of Atlantic salmon in Lake Ontario entered the lake during a post-glacial marine invasion and that their descendants continued to live in the lake, apparently without reproductive migrations to the sea (MacKay 1969).

Despite the fact that Atlantic salmon were once abundant in Lake Ontario (Webster 1982) and supported one of the world's greatest freshwater fisheries (Parsons 1973), their numbers rapidly declined after European settlement of the region. The reasons for this decline are not known with certainty, partly because the aquatic and terrestrial environments associated with Lake Ontario were being tremendously altered by the European settlers in a very short period of time, and partly because these settlers did not closely document or investigate the decline of the Atlantic salmon populations (Smith 1890; Huntsman 1944; Smith 1995).

While it is unlikely that any single factor caused the extinction of the Atlantic salmon in Lake Ontario, it would be wise for us to consider Samuel Wilmot's (Fig. 2) first-hand description of some of the instream ecological factors involved in the decline and extinction:

> *"At the first inception of the work of salmon breeding here [at the Newcastle salmon hatchery], little if anything at all, was known in relation to it in America. The idea entertained by the originator of the novel undertaking was that, as the creek was known to be formerly a salmon-breeding stream, naturally, no special reason could be well given why these fish could not be reared in it artificially. This latter view of the matter has been most practically and satisfactorily demonstrated. The stream in question had, however, became thoroughly changed from its normal state, when salmon in the olden times so largely inhabited it for spawning purposes. Then it was amply supplied with a flow of fine, cold, limpid water; the forest, from the source of the stream, all the way to its outlet into the lake, was in its primeval state, overshadowing it from the sun's rays and influences. This, with the multitude of springs of icy cold water oozing out here and there, and little rills trickling along the ever-shaded surface of the earth, together with the constantly splashing current against logs and fallen trees, gave both aeration and hiding places innumerable for the fish. These obstacles and brushwood also prevented the gravelly beds in the stream from being shifted or carried away by the force of freshets. All these were nature's provisions for assisting these migratory fishes in the reproduction of their species. But now the forest has all disappeared by the labour of the husbandman, laying bare the face of the country to the rays of the sun and general influences of the atmosphere, which by the process of absorption and evaporation have almost wholly dried up the numerous springs and rills, which were the original feeders of the creek. This has also diminished the flow of water fully one-half, and increased its temperature to such an extent during the spring and summer months as to create enormous quantities of infinitesimal spores for growth of fungi and other deleterious matter.*
>
> *In addition to the above must be mentioned the ungovernable force and destructive consequences of immense feshets [sic] that frequently prevail, rushing down the now unimpeded course of the stream, carrying away previously formed spawning grounds, sweeping along with its violence the offscourings from lately ploughed fields, and from turnpike roads, together with rotten vegetable substances from barn yards, compost heaps and other depositories of foul matter, and the refuse from saw mills and other manufactures erected upon the stream.*

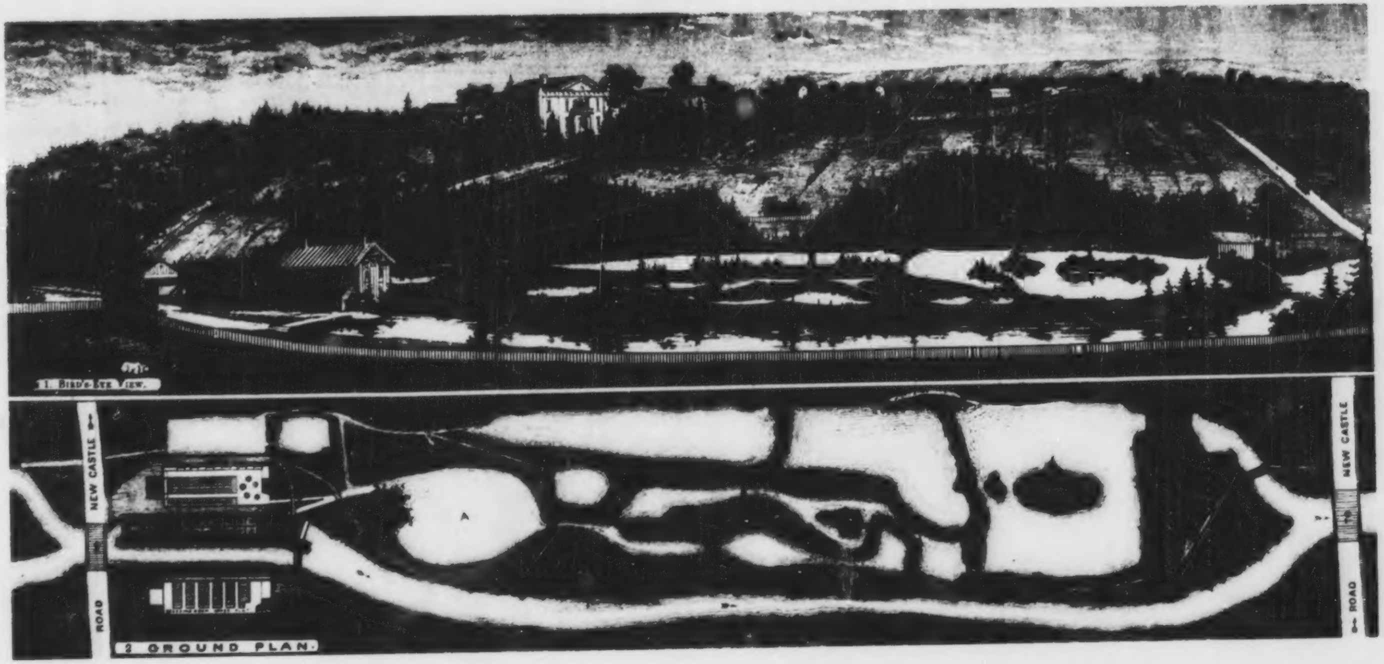
Fig. 2. Portrait of Samuel Wilmot (circa 1875), inventor and 1866 founder of the pioneering fish-breeding establishment on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario. Wilmot built the hatchery facility in an unsuccessful attempt to save the native Atlantic salmon (*Salmo salar*) in Lake Ontario from extinction. In 1874 Wilmot and Seth Green, an American counterpart, used their Lake Ontario hatcheries to undertake the first recorded introductions of non-native salmonines (i.e., chinook salmon, *Oncorhynchus tshawytscha*; rainbow trout *O. mykiss*) to the Laurentian Great Lakes. Photo source: Diana Grandfield, great granddaughter of Samuel Wilmot (Port Hope, Ontario).

> *This turbid and dangerous state of the water in this stream (and it is the same in all others in the populous parts of the country) invariably takes place just previous to, or immediately at, the critical time in the spring of the year when the fry are emerging from the eggs, and the difficulties referred to cannot be overcome, cannot be even ameliorated in the course of natural reproduction. And although the difficulties and damages resulting therefrom can be overcome by the artificial methods of propagation, nevertheless the operation is attended with much labour and anxiety, for in this state of the water, lasting a fortnight or more at a time, cleansing, by means of filtrature, is found to be quite impossible. The foul particles of sediment permeate everywhere, covering the eggs at times during the course of a few hours, to the depth of half an inch with a muddy mixture of putrid earthy and vegetable matter; this insidious substance clings to the eggs with great tenacity and cannot be removed except by means of artificial cleansing. These and other causes, which neither time nor space will admit of entering into here fully, had well nigh exterminated the salmon from the waters of Ontario. But the object of mentioning in detail some of the difficulties which do prevail, and which go towards the reduction as well as destruction of the better kinds of food fishes natural to the streams and lakes of the country, is to show that even with the many besetting drawbacks which must necessarily arise from the carrying on of various industries and from the changed state of nature in many ways in the country, a remedy to a certain extent has been instituted through the instrumentality of your Department [of Marine and Fisheries], in the selection upon this stream of a well-timed and commodious artificial fish-breeding establishment.*
>
> *This institution has already inaugurated a new industry in the Dominion, and has practically demonstrated the feasibility of a science for overcoming many of the inevitable disadvantages referred to in the fact of having reared and distributed many millions of salmon fry, and of other valuable kinds of fish, and also of introducing the salmon of the Pacific Ocean into the waters of Ontario. From the many practical experiments which have originated from this establishment in the perfecting of machinery and apparatus to simplify and economise labour and expense in the carrying out of this enterprise, a systematization of the methods of propagating fish by artificial means has been widely extended, not only in the several Provinces of the Dominion of Canada, but throughout the whole of America."* (Wilmot 1878, p. 16)

A century later, MacCrimmon (1977) looked back at the general ecological factors likely associated the demise of Lake Ontario Atlantic salmon, both instream and open-lake:

> *"Changing land and water use practices of the nineteenth century undoubtedly altered greatly the suitability of stream environments for reproduction and juvenile life of the [Atlantic] salmon. The clearing of forested land for pioneer agriculture greatly increased surface runoff, caused stream flooding and reduced summer flows, deposited smothering silt on spawning and nursery grounds, and modified natural thermal regimes. Mill dams barred would-be parent spawners from many breeding areas; newly-established communities contributed organic and industrial pollutants to previously unimpaired waterways. Coupled with the unfortunate consequences of environmental devastation was the factor of increased exploitation by commercial lake fishermen and, especially, by undisciplined persons who pirated the runs for parent fish returning to natal streams. Under the stress of reduced habitat and deteriorating environmental quality, it is most likely that overfishing played a significant role in*

Fig. 3. Bird's-eye view and ground plan of Samuel Wilmot's pioneering fish-breeding establishment on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario — circa 1877. This facility, established in 1866, was the first government-operated fish hatchery in North America, the earliest site of native Atlantic salmon (*Salmo salar*) restoration efforts on Lake Ontario beginning in 1866, and the site of the first introduction of a Pacific salmonine (chinook salmon, *Oncorhynchus tshawytscha*) to the Laurentian Great Lakes drainage basin. Source: Wilmot (1878).



> *finally sealing the doom of the Ontario [Atlantic] salmon. Attack by the sea lamprey, which was later to decimate lake trout populations in the Great Lakes, cannot be overlooked, as the eel was a known parasite of the [Atlantic] salmon as early as 1851. In the face of a changing environment and intensive fishing, even extensive releases of hatchery-reared fish failed to do more than delay the extinction of the legendary [Atlantic] salmon."* (MacCrimmon 1977, p. 89)

Smith (1995) and Ketola et al. (2000) discussed these, and other, hypothesized factors that may have been associated with the extinction of Atlantic salmon in Lake Ontario. Whatever the specific cause(s), it is clear that the decline of native Great Lakes Atlantic salmon in Lake Ontario was associated with activities of the early European settlers (Webster 1982).

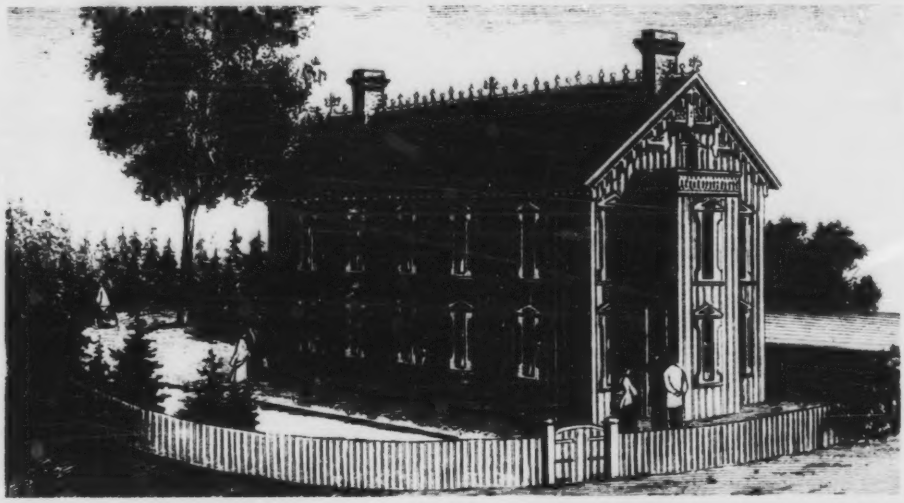
In an attempt to prevent the extinction of Atlantic salmon in Lake Ontario, both American and Canadian governments authorized the construction of facilities intended to re-establish wild populations — presumably for the purpose of revitalizing the failing food, commercial and sport fisheries (MacCrimmon 1965). Beginning in 1866, Samuel Wilmot (Fig. 2) established a fish-breeding establishment on a creek that flowed through his property in southern Ontario (Figs. 3, 4); this was the first

Fig. 3 (*concluded*). Samuel Wilmot's description of these images:

> "[The top panel] *is a panoramic view of the building and grounds, and of the surrounding country. The building on the left of the picture, on the edge of the stream, is the Government fish-breeding establishment, with its long, low reception house alongside; just here a permanent weir or carrier is thrown across the stream, which prevents the upward passage of the salmon. Being thus stopped on their progress up the main channel, they are attracted by the rapid outflow of water coming through the reception house, and rushing up the current they pass through an ingeniously-contrived triangular-shaped weir* [see Fig. 5], *and become entrapped within the house where they are kept confined till they become ripe for spawning. From this building the stream runs (along the side of the picture) down a distance of some two miles, where it empties into Lake Ontario.*
>
> *Beneath the two large clumps of evergreen trees, in front of the middle and the main stream, the several nurseries and retaining ponds are shown, dotted here and there with miniature islands. In some of these ponds the parent salmon are retained for a while to recuperate after the exhaustion produced by spawning; others are used as nurseries in which the young fry are kept for a time just after they are hatched out, and have absorbed the umbilical sac.*
>
> *The small building to the extreme right of the view was the old or original reception house, but it is now used as the gateway and general outlet from the ponds. On the extreme left, just above the main building, is an old mill with its raceway and mill-pond beyond. From the higher elevation of this large reservoir a sufficient head is obtained to force through an underground pipe a large flow of water into the first and second apartments or breeding-rooms; thus giving a constant and sufficient supply at all times for the hatching troughs.*
>
> *The premises and ponds cover some ten acres of land. Two public roads lead from the grounds, one at each extremity of the picture, and converge together at the village of Newcastle, about three-quarters of a mile distant, where an important station of the Grand Trunk Railway is located. The town of Bowmanville is situated about four miles to the west, and the town of Port Hope seventeen miles to the east.*
>
> *On the summit of the mill is my own farm and residence."* (Wilmot 1878, p. 24)

Fig. 4. Main building ("reception house") at Samuel Wilmot's pioneering fish-breeding establishment for Atlantic salmon (*Salmo salar*) and chinook salmon (*Oncorhynchus tshawytscha*) on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario — circa 1877. Source: Wilmot (1878).

> "[The illustration] *shows the front and side elevation of the fish-breeding house proper; its dimensions are 64 ft. in length by 22 ft. in width, with a cellar or lower flat built of stone, and two frame stories above ground. The building presents a handsome and commanding appearance externally, and the arrangements inside are convenient and well adapted for the purposes for which they are intended. The whole establishment gives convincing proof throughout of the exercise of practical ingenuity and personal industry.*" (Wilmot 1878, p. 25)



government-operated fish hatchery in North America (MacCrimmon 1965, 1977). Hatchery personnel stripped the gametes of surviving adults, and reared the offspring under artificial conditions before releasing them back to the tributaries or open water (Figs. 5–11). From 1867 to 1883, hatcheries planted Atlantic salmon juveniles in numerous tributaries to Lake Ontario; however, none of these attempts led to the re-establishment of self-sustaining wild populations (Smith 1890; Fox 1930; MacKay 1969). By 1900, the Atlantic salmon of Lake Ontario were extinct.

Thus far, we have considered only the attempts to re-establish Atlantic salmon to a Great Lake in which it was native. However, the efforts of the early fish culturists were not limited to Lake Ontario:

> *"Efforts to establish the Ontario [Atlantic] salmon in other waters date back to the heyday of the Newcastle Hatchery [i.e., 1866–1878], when plantings of young salmon were made in the watersheds of lakes Erie, Huron and Simcoe. As well, attempts were made, principally by United States agencies, during the last quarter of the nineteenth century to establish anadromous and landlocked [Atlantic] salmon from Quebec, New England and the Maritime provinces in waters of all the Great Lakes. Numerous releases of sebago and ouananiche salmon were made. Despite these many plantings, the [Atlantic] salmon was absent from Ontario waters at the beginning of the twentieth century."* (MacCrimmon 1977, p. 88)

Fig. 5. Fish entrapment and holding facilities inside Samuel Wilmot's pioneering fish-breeding establishment for Atlantic salmon (*Salmo salar*) and chinook salmon (*Oncorhynchus tshawytscha*) on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario — circa 1877. Source: Wilmot (1878).

> This illustration depicts the *"inside arrangements of the reception house for entrapping and penning up the parent salmon. The fish enter this building through the triangular-formed weir, and become imprisoned in the first or large compartment. They are afterwards transferred (as represented by the assistant dipping them out with a small net) into the smaller pens above. The males and females are then separated and placed in different pens; in this way they remain quiet, and are more easily retaken at the time when they become ripe for laying their eggs."* (Wilmot 1878, p. 24)
>
> *"When mature, a dozen or more of these fish at one time are again caught with the hand net, and carried (only a few feet) to their tanks arranged for their safe keeping at the right hand side of the breeding-room, lower flat; where the workmen are engaged at their work. Here the process of taking the ova from the fish and impregnating it is carried on ... After this operation is performed, she is liberated by dropping her into a raceway running from the room, down which she quickly swims into the pond,* (marked A, on the ground plan [see Fig. 3]). *A male fish is then taken from another tank, and operated on in a like manner as the female;... The ova are then dipped out of the pan with a small ladle, and put into a measure made to contain one thousand eggs; from this they are spread evenly on the hatching trays* [see Fig. 6]. ... *These trays are made two feet long and ten inches wide, with a division in the centre, and hold four thousand eggs each; when filled they are carefully laid in the breeding troughs [shown in top and bottom panels]. After the ova are thus deposited they are closely watched, and regularly cleansed from all sediments or other impurities which may settle upon them during the process of incubation. The eggs are of a clear salmon color, but should any prove to be unfertilized, or become injured in any way, they change their appearance to an opaque white, when they are picked out with forceps and cast away, thus preventing the remaining ova from becoming contaminated.* [These illustrations] *explain the manner in which the breeding troughs are distributed in the rooms. In the lower flat they are placed lengthwise, in the upper room crosswise of the building. Six of these are laid side by side with intervening aisles two feet wide for the convenience of the workmen in picking and washing the eggs. The troughs are each supplied with a constant flow of living water from the tanks which are fed from the raceway above, and are regulated in quantity by wooden taps, as shown in the cut. In the lower flat a series of aquaria are shown; they are placed alongside the wall and contain young salmon and other fish which are kept for observation, and also for exhibition, to the numerous visitors who frequent the institution."* (Wilmot 1878, p. 24)

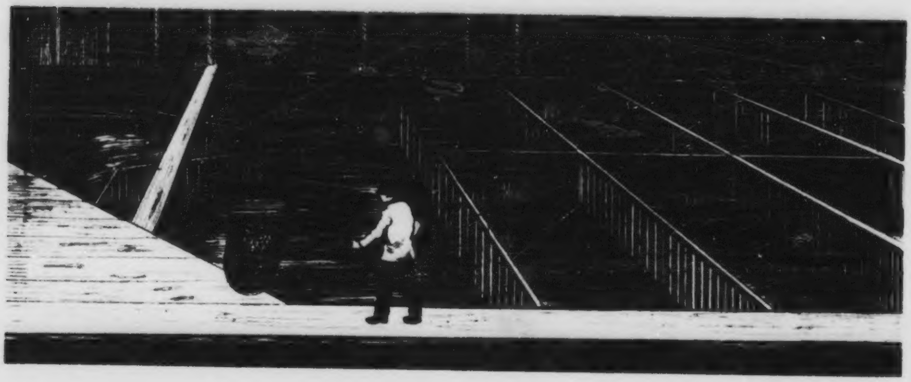
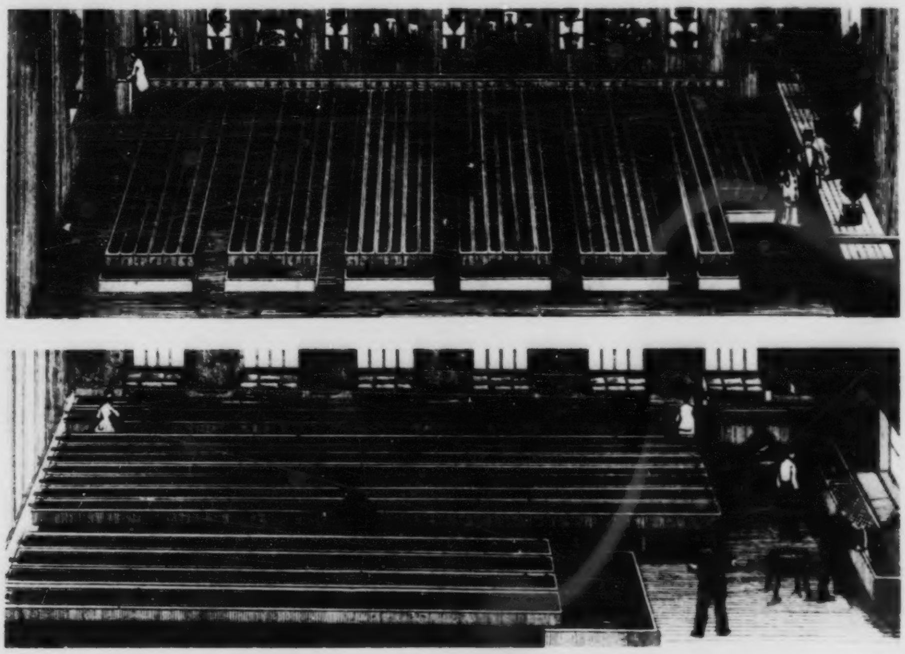


Fig. 6. Fish breeding-rooms *(top panel = upper floor, bottom panel = lower floor)* inside Samuel Wilmot's pioneering fish-breeding establishment for Atlantic salmon (*Salmo salar*) and chinook salmon (*Oncorhynchus tshawytscha*) on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario — circa 1877.



In 1873, both American and Canadian governments attempted to introduce Atlantic salmon across the Great Lakes, including those which did not previously have this species as part of the native community (Emery 1985; Keller et al. 1989). While the objectives for such introductions were poorly documented, it can be assumed that the Atlantic salmon was intended to support fisheries in these waters. No specific concern was apparently expressed about the possibility of negative effects that could result from such introductions.

Despite the lack of success resulting from these early introductions, repeated attempts were made to establish Atlantic salmon in the upper Great Lakes:

> *"Failures of the nineteenth century did not totally discourage further interest in creating [Atlantic] salmon fisheries in Ontario waters. Plantings were made between 1910 and 1913 in Lake Superior and Georgian Bay tributaries and in a number of inland waters including Lake Simcoe and lakes in Algonquin Park and Muskoka."* (MacCrimmon 1977, p. 89)

Between 1935 and 1939, Atlantic salmon were once again introduced to the Great Lakes and numerous inland waters (OMNR 1995); however, the only self-sustaining population to result from these actions was in Trout Lake near North Bay, Ontario (MacKay 1969). In 1953, New York State again released Atlantic salmon into lakes and headwater tributaries of Lake Ontario (Parsons 1973). While this stocking

Fig. 7. Gamete stripping and fertilization at Samuel Wilmot's pioneering fish-breeding establishment for Atlantic salmon (*Salmo salar*) and chinook salmon (*Oncorhynchus tshawytscha*) on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario — circa 1877. Source: Wilmot (1878).

> "*... the process of taking the ova from the fish and impregnating; ... this is done by lifting from the tank a ripe female fish and holding her over a vessel securely, and gently pressing her body with the hand when the eggs will flow freely from her. ... A male fish is then taken from another tank, and operated on in a like manner as the female; the milk extruded from him is mixed with the eggs by a gentle stirring with the hand; this causes immediate impregnation.*" (Wilmot 1878, p. 25)

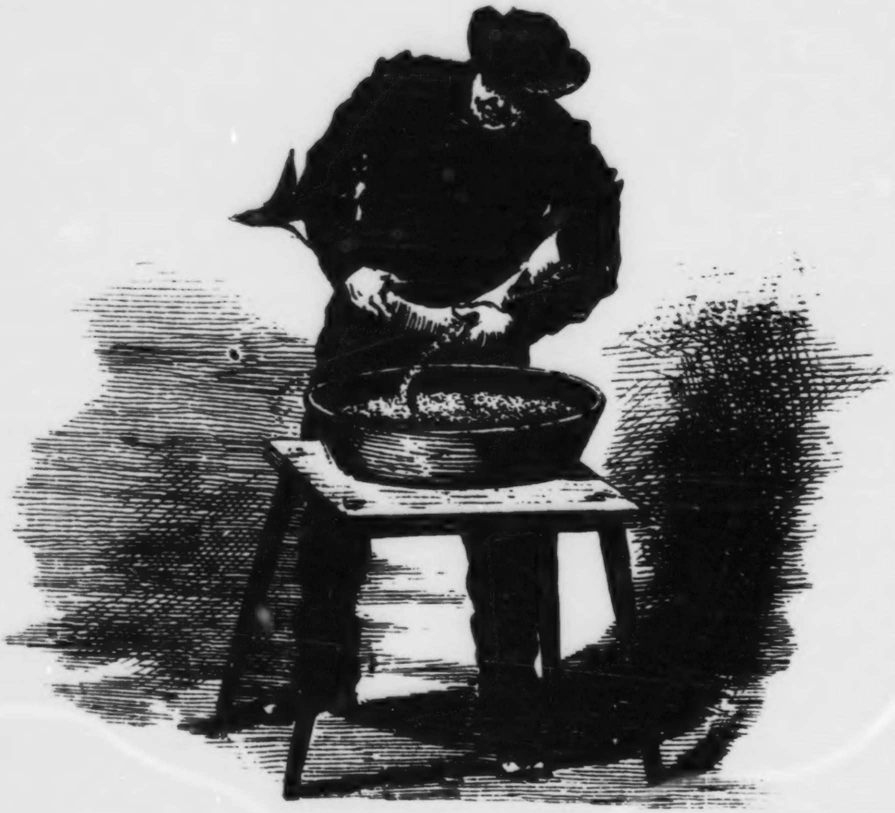
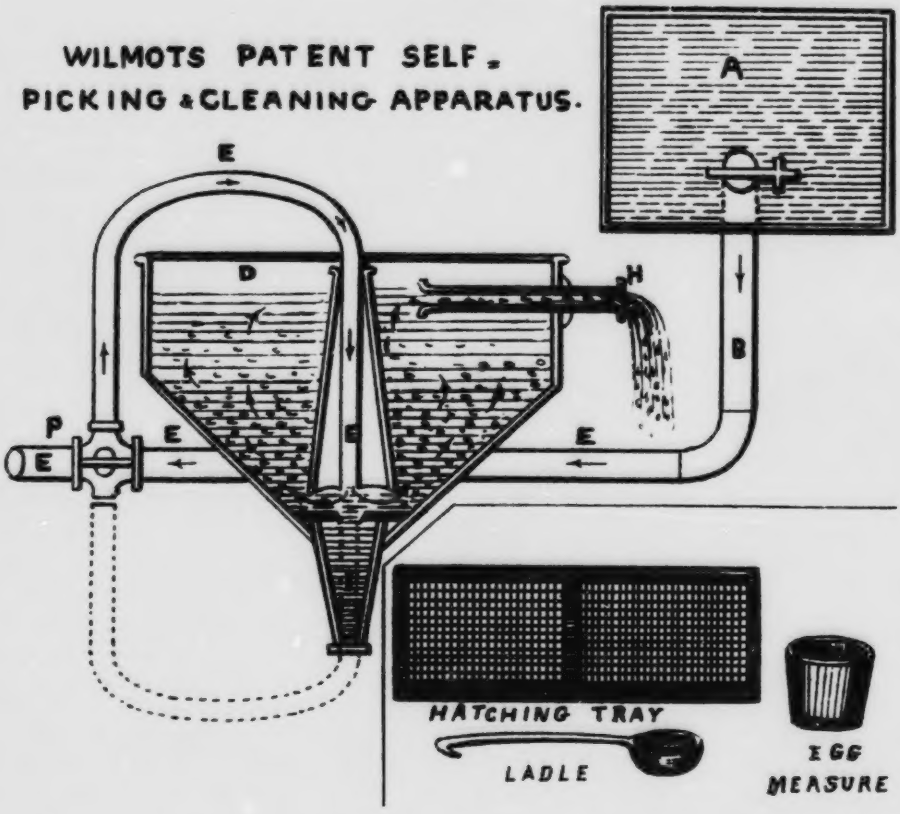


Fig. 8. "Wilmots Patent Self-Picking & Cleaning Apparatus" used at Samuel Wilmot's pioneering fish-breeding establishment for Atlantic salmon (*Salmo salar*) and chinook salmon (*Oncorhynchus tshawytscha*) on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario — circa 1877. This apparatus was invented to separate living from contaminated or dead embryos in the hatching trays. Source: Wilmot (1878).


WILMOTS PATENT SELF-PICKING & CLEANING APPARATUS.
A
E
D
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B
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E
HATCHING TRAY
LADLE
EGG MEASURE

program established populations large enough to support a small recreational fishery, the fish apparently did not reproduce (Emery 1985). By 1958, all introduced Atlantic salmon in the Great Lakes basin were considered either exceptionally rare, or extinct (Hubbs and Lagler 1958).

In general, the Atlantic salmon was not the subject of intensive stocking efforts during the recent era of Great Lakes salmonine introductions. However, stocking of this species has occurred on a limited basis in some areas:

> *"Interest in re-establishing the Atlantic salmon in the Great Lakes will probably never die as various agencies, currently the States of Michigan and Wisconsin, make token plantings with, as yet, only fragmentary evidences of success."* (MacCrimmon 1977, p. 90)

In the opinion of some fisheries managers, Atlantic salmon have prohibitively stringent reproductive requirements, including very particular stream substrate qualities (e.g., Tody and Tanner 1966).

From 1972 to 1998 the Province of Ontario and the States of Michigan, Wisconsin and Minnesota obtained Atlantic salmon from Quebec, Maine, Sweden and elsewhere (Emery 1985; Keller et al. 1989; Behmer et al. 1993). Of these, approximately 2.7 million fish were re-introduced to Lake Ontario — mostly by American fisheries agencies (Fig. 13, Appendix I). Approximately 1.5 million Atlantic salmon have been introduced to Lakes Huron, Michigan and Superior (Fig. 14, Appendix I). Some of these stocking programs, such as the introduction of Atlantic salmon from West Grand Lake, Maine to the St. Marys River, continue to support local sport fisheries (Behmer et al. 1993). Taken as a whole, 100% of all Atlantic salmon introduced to the Great Lakes ecosystem (i.e., other than Lake Ontario) in the modern era have been released by American hatcheries.

There have also been some renewed efforts by fisheries managers to re-establish Atlantic salmon in its native Lake Ontario (e.g., OMNR 1995). However, the Ontario government has decided that while the booming recreational salmon fisheries in Lake Ontario will continue to receive strong provincial support, a full Atlantic salmon restoration program for Lake Ontario cannot proceed due to financial constraints. At present, the Ontario restoration program is limited to a couple of instream investigations "about which factors may limit successful restoration of Atlantic salmon." The factors that are currently considered important to Atlantic salmon restoration in Lake Ontario include (1) instream habitat suitability for juveniles and spawning adults and, (2) competitive interactions between Atlantic salmon and introduced salmonines, namely chinook salmon, coho salmon, rainbow trout and brown trout (Fig 1., OMNR 1995).

Fig. 9. Illustrations of Atlantic salmon (*Salmo salar*) ontogeny, based on work at Samuel Wilmot's pioneering fish-breeding establishment on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario — circa 1877. Source: Wilmot (1878).

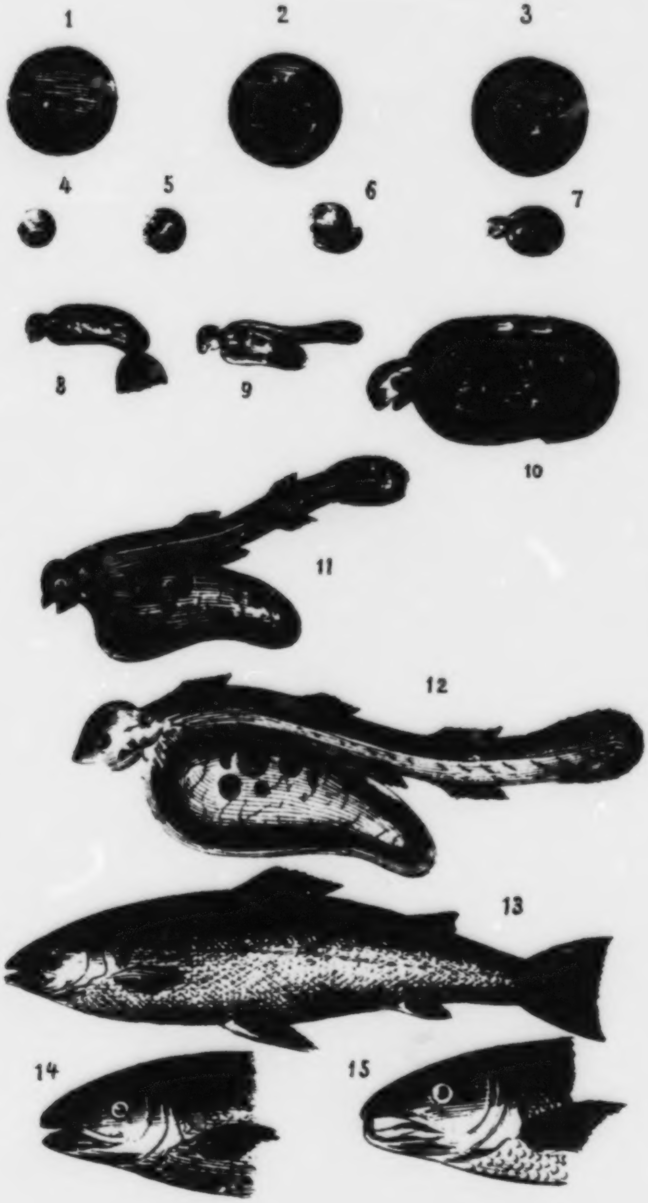


Fig. 9 (*concluded*).

"[This illustration] *gives views of the several shapes of the eggs during incubation and the growth of the embryo. Explanation:*

No. 1. *Shows the young ova developing the head (magnified).*

No. 2. *Shows the young ova developed (magnified).*

No. 3. *The head and body of the fish developed (magnified).*

No. 4. *Young ova before the developing, in natural size.*

No. 5. *Shows the ova of the natural size, after the vital principle has been developed. The body of the fish in this state has a pinkish tinge and the eyes are very large.*

No. 6. *The shell of the ovum just burst, and the head of the fish protruding from it.*

No. 7. *The state of the ovum shown after the bursting of the shell, when the pulsations of the heart become visible.*

No. 8. *The shell just thrown off; the tail drooping; about a third part of the shell, which is transparent, is fractured by the fish in its exertions to extricate itself. Before the shell is broken the tail envelopes the yoke, which is seen attached to the body of the fish.*

No. 9. *The tail in a short time becomes straight and the fish, more lively, the mouth assumes a different form, and the lower and pectoral fins, which are quite transparent, are in motion simultaneously with the actions of the heart, which beats from 60 to 65 times in a minute.*

No. 10 *is a magnified representation of No. 7, the fish adhering to the shell, which is partly broken.*

No. 11 *represents No. 9 magnified; the heart is before the pectoral fins under the throat.*

No. 12 *is a still more enlarged view of No. 9, showing the direction in which the blood circulates, as seen by a microscope. The blood flows from under the body of the fish through the blood-vessels ramified along the sides of the back, and is there collected into a large vessel which runs along the front and bottom of the bag, communicating directly with the heart. An equal quantity of air or some transparent matter circulates with the blood. The blood is drawn by the heart from the large vessel alluded to, and thrown into regular pulsations into the vessels of the heart and throat where it assumes a dark colour. The rays of the gills are visible, and the fish soon begins to assume a brownish colour.*

No. 13 *Salmon, developed shape.*

No. 14 *Salmon, general appearance in proper season.*

No. 15 *Salmon (male) at the spawning season.*" (Wilmot 1878, p. 26)

Fig. 10. Retaining ponds at Samuel Wilmot's pioneering fish-breeding establishment for Atlantic salmon (*Salmo salar*) and chinook salmon (*Oncorhynchus tshawytscha*) on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario — circa 1877. Source: Wilmot (1878).

> "[This illustration] *gives a view of one of the retaining ponds* (marked A, [Fig. 3]) *into which the spent salmon pass from the main building after manipulation. It is about forty feet in diameter and circular in form, with an average depth of water from two to three feet. At the time this view was taken there were in this pond between three and four hundred adult salmon, weighing from six to sixteen pounds each. It is doubtful, indeed, whether in any other part of the world a more wonderful or pleasing exhibition can be enjoyed at one sight, of such numbers of large salmon as were enclosed within this small space. This extraordinary display is not of long duration, lasting only about a fortnight, generally during the last week of October and first week or November."* (Wilmot 1878, p. 25)

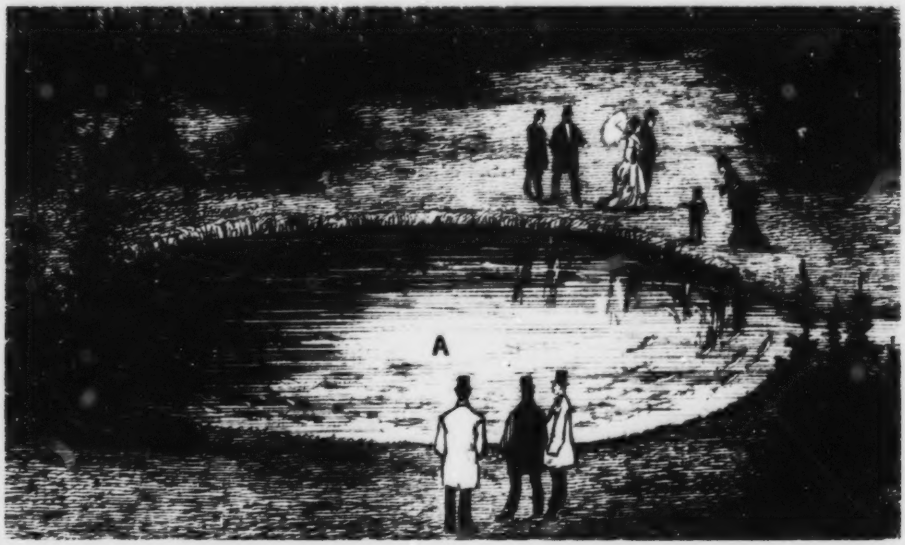


Fig. 11. Natural history museum at Samuel Wilmot's pioneering fish-breeding establishment for Atlantic salmon (*Salmo salar*) and chinook salmon (*Oncorhynchus tshawytscha*) on Wilmot's Creek (Lake Ontario basin) at Newcastle, Ontario — circa 1877. Source: Wilmot (1878).

> "[This illustration] *represents the upper story of the building, which, after taking from it office rooms, leaves a large commodious apartment used as a museum, in which are collected a number of specimens of fish of various kinds and other animals. This natural history depository is only of a few months' existence; yet it comprises numerous specimens of the salmon family and other fish, prominent among which are the large ones shown in the plate; the one on the right is a sturgeon weighing 280 lbs.; the one on the left is the tunny or giant mackerel; its weight when alive was upwards of 600 lbs.; a Greenland shark ten feet long, an immense moose deer, male and female cariboo, a bear and other animals; also an alligator ten feet long. All these specimens present a life-like appearance and are artistically mounted.*" (Wilmot 1878, p. 25)

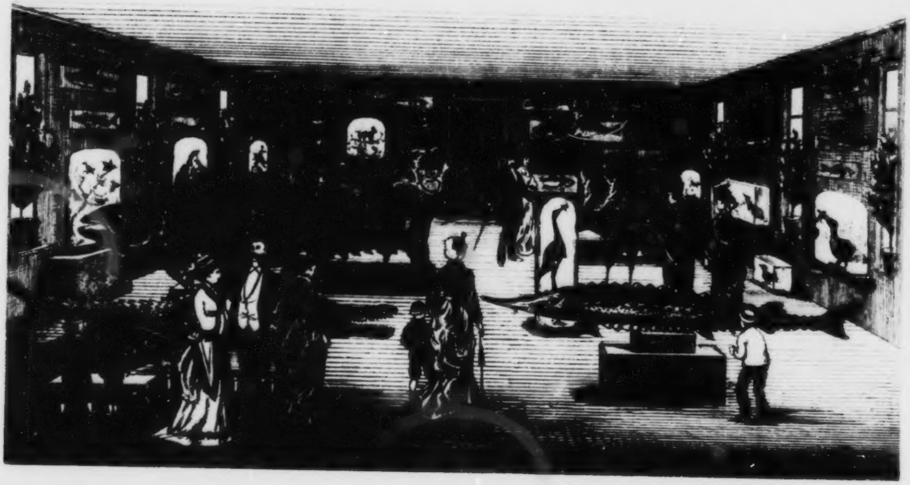


Fig. 12. Michigan State Fish Hatchery at Sault Ste. Marie, Michigan — circa 1890. Operating in the 1890s, this facility reflects the rapid dispersion and extension of the hatchery technology developed by Wilmot at the pioneering Newcastle fish-breeding facility established in 1866.

> *"[The Newcastle hatchery] has already inaugurated a new industry in the Dominion, and has practically demonstrated the feasibility of a science for overcoming many of the inevitable disadvantages referred to in the fact of having reared and distributed many millions of salmon fry, and of other valuable kinds of fish, and also of introducing the salmon of the Pacific Ocean into the waters of Ontario. From the many practical experiments which have originated from this establishment in the perfecting of machinery and apparatus to simplify and economise labour and expense in the carrying out of this enterprise, a systematization of the methods of propagating fish by artificial means has been widely extended, not only in the several Provinces of the Dominion of Canada, but throughout the whole of America.*" (Wilmot 1878, p. 16)

Photo credit: A.E. Young, Sault Ste. Marie Michigan and Sault Ste. Marie, Ontario (from "The Soos of To-day, American and Canadian" ca. 1890; Published by W.G. MacFarlane, Toronto, Canada).

Fig. 13. Number of Atlantic salmon (*Salmo salar*) stocked by jurisdiction in Lake Ontario for the period 1966–1998.

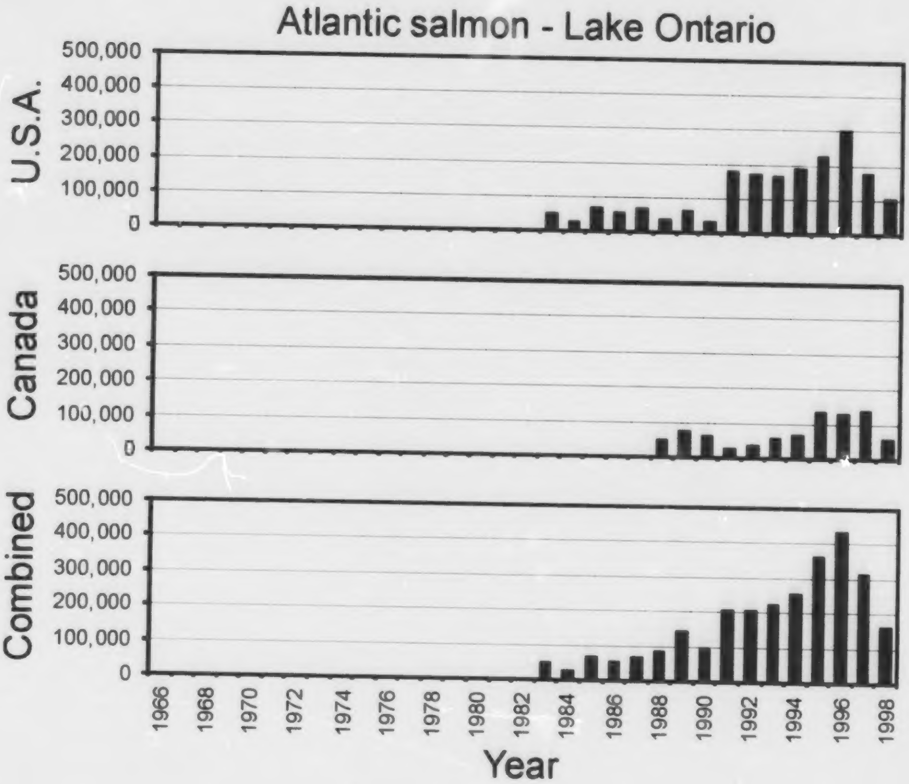
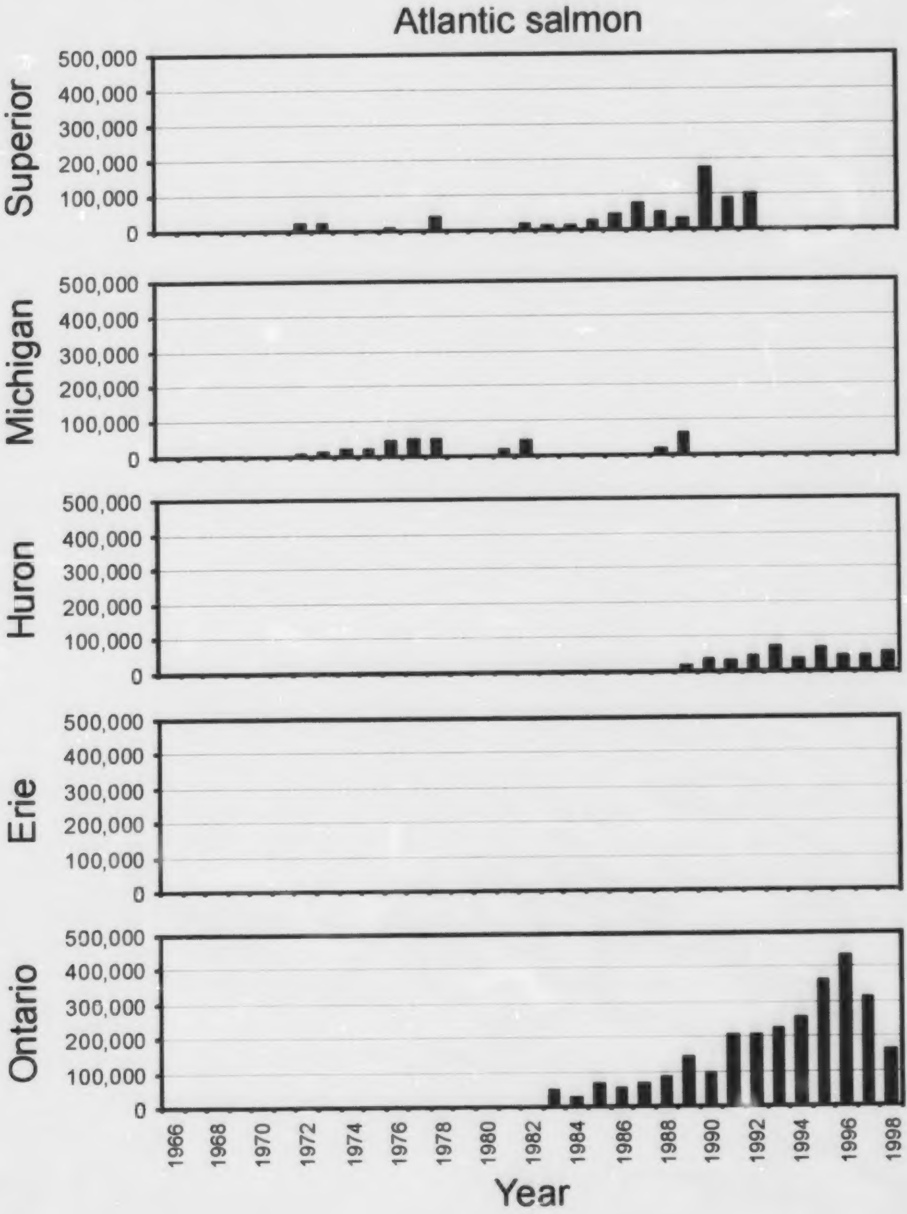


Fig. 14. Number of Atlantic salmon (*Salmo salar*) stocked in each of the Laurentian Great Lakes for the period 1966–1998.



2.1.2 Brown trout (*Salmo trutta*)

The brown trout (Fig. 15) is native to waters of Europe and western Asia. The natural distribution of this species extends from Afghanistan westward throughout Europe to the Atlantic Ocean; extending to Mediterranean drainage basins, alpine lakes and streams, the British Isles and Scandinavia (MacKay 1969; Scott and Crossman 1973; MacCrimmon 1977).

The first importation of brown trout to North American fish hatcheries occurred in 1883–1884, when brown trout eggs originating from Europe were shipped to the United States (Crossman 1968; MacKay 1969). The first brown trout strains introduced to North America were from Scotland's Loch Levan (courtesy of Sir Ramsey Maitland and the Howietown Hatchery in Stirling) and the so-called 'German brown trout' from the upper Danube River (courtesy of the German fish culturist, von Behr) (MacCrimmon and Marshall 1968; MacKay 1969; MacCrimmon et al. 1970).

The first introduction of brown trout to the Great Lakes drainage basin is attributed to the Americans, and occurred shortly after the species arrived on the continent:

> *"European brown trout were first released into the Great Lakes basin in 1883 when Michigan stocked the Pere Marquette River, a Lake Michigan tributary (Emery 1985). In the same year, an accidental release from a fish hatchery in Caledonia, New York, occurred into the Genesee River, a tributary to Lake Ontario."* (Mills et al. 1993, p. 11)

Following these original introductions, brown trout were also cultured from other Eurasian 'strains' (e.g., sea trout, Swiss lake trout, Ohrid trout, Harrietta browns) and were released across the Great Lakes (Keller et al. 1989). Apparently, the early fish culturists experienced difficulty in keeping these 'strains' separated in their hatcheries, and this has somewhat confused the actual pedigree of most brown trout stocks in North America (MacCrimmon 1977).

The early objectives for brown trout introductions appear to be directly linked to the newly-constructed fish hatcheries that were springing up throughout the Great Lakes:

> *"Early enthusiasm for introducing the brown trout to North America was generated principally by the fish culturists themselves. The species was easily cultured in their trout hatcheries and it was fun to breed and release the various strains of this attractive exotic. As a result brown trout fisheries were created at an early date in a number of streams on the United States side of the Great Lakes."* (MacCrimmon 1977, p. 106)

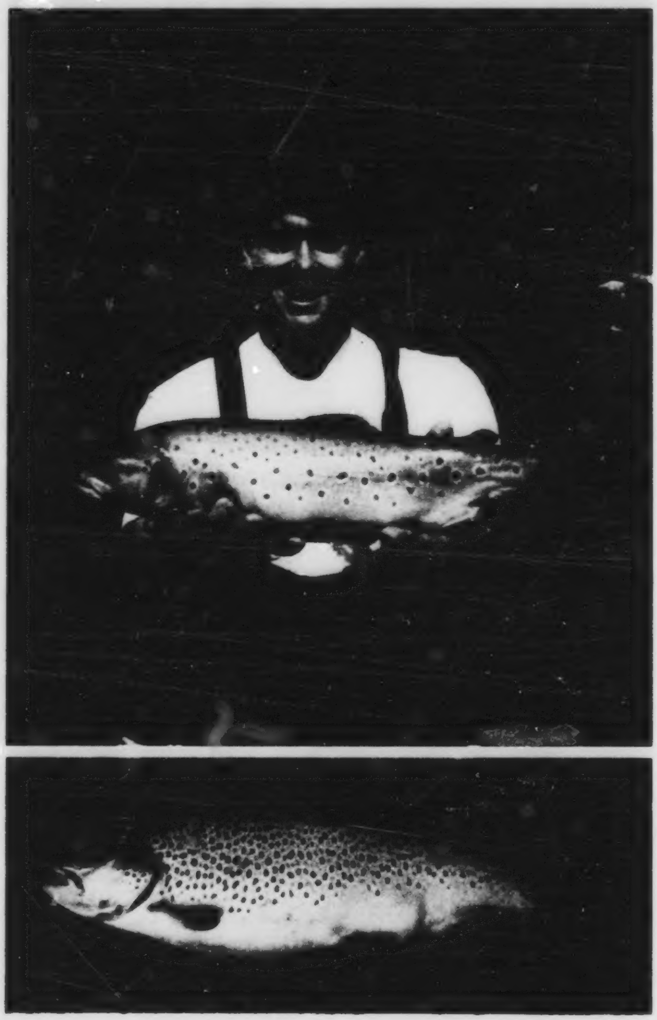
Thus, an original reason for introducing brown trout to the Great Lakes was to provide a hobby or perhaps aesthetic satisfaction for people who ran the fish hatcheries.

In contrast, anglers in the United States were not so quite pleased about the early attempts to introduce brown trout:

> *"Despite the high regard with which the brown trout was held as a sport fish in the Old World, American anglers seemed indifferent to this novel exotic, which was deemed to be harder to catch than the prized native brook or speckled trout."* (MacCrimmon 1977, p. 106)

It appears that the original introduction of brown trout to the Great Lakes actually became the subject of much controversy among anglers. The major issue in this controversy was a concern held by many anglers that the introduced species would

Fig. 15. Brown trout (*Salmo trutta*) introduced to the Laurentian Great Lakes drainage basin. *Top photo*: Stream-resident brown trout sampled with electro-shocking gear from D'Aubignay Creek (Grand River watershed, Lake Erie basin) in 1991. *Bottom photo*: Ripe, stream-resident, female brown trout angled from Bronté Creek (Lake Ontario drainage basin) in October 1991. Photo credits: Chris Weland.



threaten native species that were highly valued within the early recreational fisheries, notably the brook charr:

> "*It was not until trophy brown trout started to appear in anglers' catches that the species began to make the headlines. Each year progressively larger trout were being taken and, at the turn of the century, the record fish was a 3.9 kg specimen taken from an Ohio tributary of Lake Erie. While some fishermen were jubilant, others condemned the species as a serious threat to the welfare of native brook trout, which they viewed as a natural heritage to be enjoyed and preserved.*" (MacCrimmon 1977, p. 106)

> "*The angling fraternity had become irreparably divided on the advisability of making further plantings of brown trout by the 1880's by which time an estimated five million fish had been released in waters of those states bordering on the Great Lakes.*" (MacCrimmon 1977, p. 107)

This division among the recreational anglers led to a temporary halt of brown trout stocking in the Great Lakes in the early 1900s; however, the advocates of brown trout introduction eventually managed to convince the fisheries management authorities to resume their stocking programs (MacCrimmon 1977).

Although poorly documented, it appears that one of the chief factors involved in the acceptance of early brown trout introductions to the Great Lakes was related to habitat deterioration in the tributaries. In general, brown trout are considered to have the same habitat requirements as the native brook charr: clean, cold water with access to gravel spawning beds (Scott and Crossman 1973). However, brown trout exhibit a greater ability to survive and reproduce in warmer and fouled waters that result from deforestation, damming, agriculture and urbanization:

> "*Justification for using the brown trout for sport fishing was based on its greater tolerance for warm-water environments than the native brook trout possessed. Although the actual differences in lethal temperatures between the two species was small, the exotic was able to survive in many miles of streams in which the brook trout could no longer live during the summer months. Most plantings were made, therefore, in the lower parts of stream systems from which a few survivors moved to the Great Lakes; there, like the sea trout of Europe, they grew large on an abundance of forage fishes. However, it was those trout that remained in the streams which provided the essence of the American sport fishery.*" (MacCrimmon 1977, p. 107)

Thus, as was the case with Atlantic salmon native to Lake Ontario, the indirect effects of European settlement around the Great Lakes combined to act as a critical factor in the acceptability and success of brown trout introductions. Faced with the intractable effects of human 'developments' along Great Lakes tributaries, public opinion apparently changed to favour brown trout as an acceptable alternative or supplement to native salmonines.

Up until 1900, the Province of Ontario had refrained from stocking brown trout in the Great Lakes — due largely to the public controversy about the effects of such an introduction (MacCrimmon 1977). It was not until 1913 that Ontario began its own stocking program with the intention of establishing brown trout populations in Canadian waters, beginning with releases of brood stock from Pennsylvania in the Speed River near Hespeler (Cambridge), and in streams near Simcoe and St. Paul's (MacKay 1969). By 1925, a stock of Loch Leven brown trout had been built up at the

Mount Pleasant hatchery with production in excess of one million eggs per year, most of which were released into tributaries of Lake Erie. In 1929, Ontario extended its stocking of brown trout to tributaries of Lake Ontario and Lake Huron, including Georgian Bay (MacCrimmon 1977).

The early planting of brown trout in Great Lakes tributaries established many small but self-sustaining populations throughout much of the states bordering the Great Lakes, and in waters draining the agricultural areas of southern Ontario such as the Humber, Credit, Speed, Grand, Saugeen, Sydenham and Nottawasaga rivers (MacKay 1969; MacCrimmon 1977). However, the degree of wild reproduction by brown trout was never extensive; most local populations were heavily supported by hatchery stocking programs. Few brown trout moved into the Great Lakes proper, and most of these stayed relatively close to the home streams without establishing a reputation for extensive migrations (MacKay 1969).

Some states, such as Michigan, continued to sporadically stock brown trout from 1900 to 1960 (Emery 1985). By the early 1960s, fisheries managers in the Great Lakes drainage basin re-evaluated the decision to stock brown trout in many tributaries. In 1962, the Province of Ontario terminated its brown trout stocking program, citing several factors in support of their decision including:

- low catchability of brown trout, especially of larger individuals,
- probable competition between brown trout and native brook charr,
- poor survival rates of stocked brown trout,
- inability of brown trout to sustain themselves without hatchery stocking, and
- financial costs associated with the hatchery program (MacKay 1969; MacCrimmon 1977)

As MacCrimmon (1977) noted, surprisingly little was known about the ecology of brown trout at the time that most stocking programs were terminated. Fisheries managers had little, if any, information on the status of introduced populations in Great Lakes tributaries, including the ecological effects that they caused.

The decision to give up on brown trout introductions appears to have been based largely on the general failure of the species to support a self-sustaining fishery. Some 10 million brown trout had been released in Canadian waters of the Great Lakes drainage basin between 1913 and 1960 (MacCrimmon and Marshall 1968; MacCrimmon 1977). Apparently, no major populations of wild-reproducing brown trout were established as a result of these stocking efforts.

During the recent era of salmonine introductions, there has been a renewed interest in establishing brown trout to support recreational fisheries:

> *"[Since 1960], brown trout have become increasingly popular among both anglers and biologists alike. The larger ones especially, are somewhat more*

> *resistant to angling pressure than large brook trout. They can withstand the less favourable environment of the lower reaches of streams and rivers that are unsuitable to brook trout. They grow faster and live longer than brook trout and, a larger number of year-classes are available in a stream at any one time."* (Scott and Crossman 1973, p. 200)

In a manner similar to the early era of brown trout introductions, this species was considered to be an appropriate choice for tributary waters that had originally been inhabited by brook charr, but which had deteriorated because of human activity:

> *"Because of their greater tolerance to environmental conditions and their aggressive nature, browns can displace brook trout where productive populations of the latter would otherwise continue to exist. Also, because of the predaceous qualities of large brown trout, restocking with the young of its own kind or with young of other species is impractical. Brown trout may be utilized to good advantage in larger streams where warmer temperatures have resulted from the construction of dams or the destruction of cover or both. When water is of marginal quality, and especially in the absence of facilities for reproduction, trout fishing can only be maintained by stocking legal-sized trout."* (MacKay 1969, p. 89)

Over the past decade, recreational fishing groups have largely taken on the responsibility of stocking brown trout in these tributaries (e.g., LHMU 1998).

For the period 1966–1998, more than 81 million brown trout have been introduced to the Great Lakes ecosystem (Appendix I). Modern stocking of brown trout in Lake Ontario (approximately 15 million) began sooner, and was maintained at higher levels in American waters, compared to releases by the Ontario government and sportsmen's clubs (Fig. 16). Lake Erie received less than 5 million brown trout for the same period, almost three-quarters of which were released by American hatcheries (Fig. 17). Surprisingly, Lake Huron received almost as many brown trout in the modern era (approximately 13 million) as Lake Ontario; once again, the American sources accounted for the vast majority of these ongoing introductions (Fig. 18). When viewed across the Great Lakes, it can be seen that more than half of all 81 million brown trout releases have occurred in Lake Michigan — stocking in the other lakes has been consistent, but relatively light in comparison (Fig. 19). Taken as a whole, 90% of all brown trout introduced to the Great Lakes ecosystem in the modern era have been released by American hatcheries.

Migratory brown trout do occur in the open waters of the Great Lakes (see Fig. 15); however, they are less often taken by anglers than stream-resident brown trout, and are not intensively stocked by fisheries managers for capture in the open-lake environment (Tody and Tanner 1966). There has been indication of varying degrees of wild reproduction in many brown trout populations (see Section 3.1.3); however, quantitative data upon which to base estimates of wild reproduction are generally lacking. Even in cases where brown trout do reproduce in the wild, many of these populations are hatchery-supplemented (Mills et al. 1993).

Fig. 16. Number of brown trout (*Salmo trutta*) stocked by jurisdiction in Lake Ontario for the period 1966–1998.

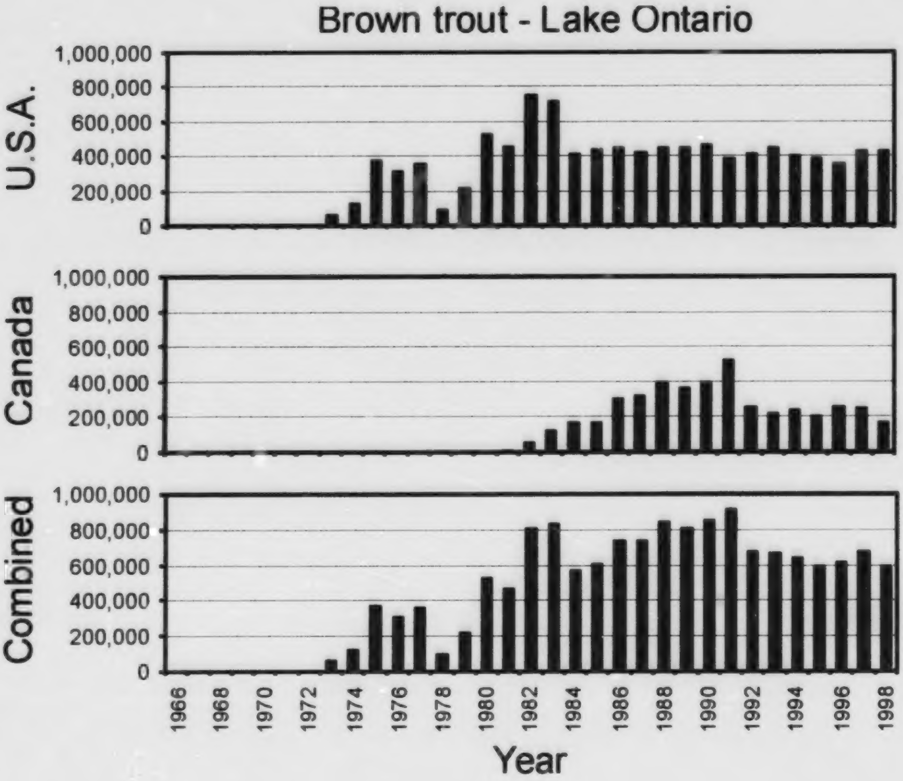


Fig. 17. Number of brown trout (*Salmo trutta*) stocked by jurisdiction in Lake Erie for the period 1966–1998.

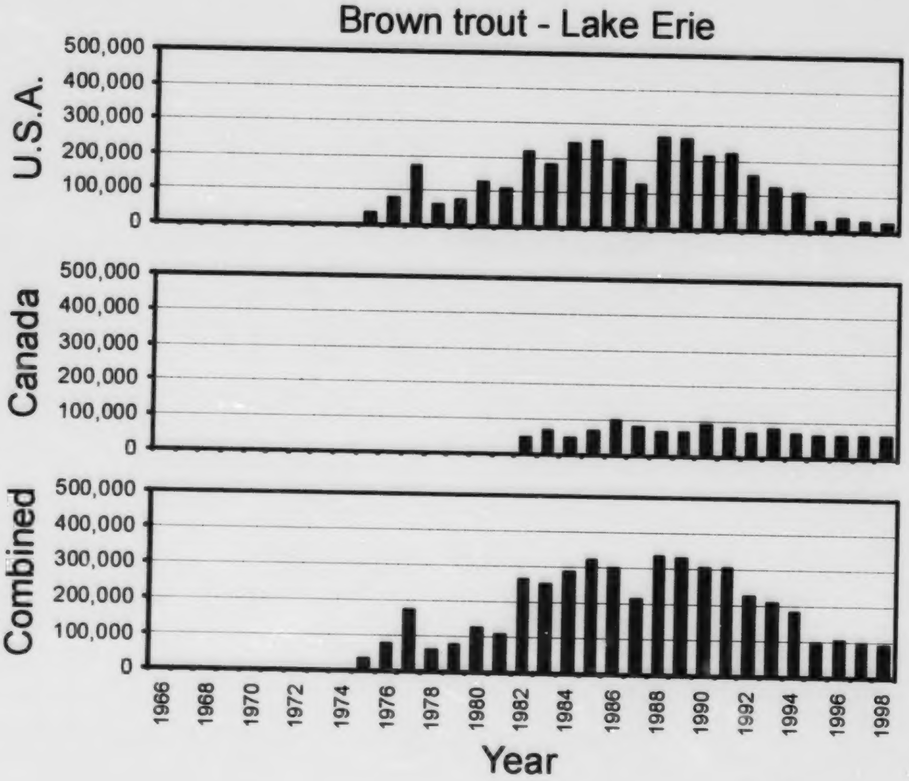


Fig. 18. Number of brown trout (*Salmo trutta*) stocked by jurisdiction in Lake Huron for the period 1966–1998.

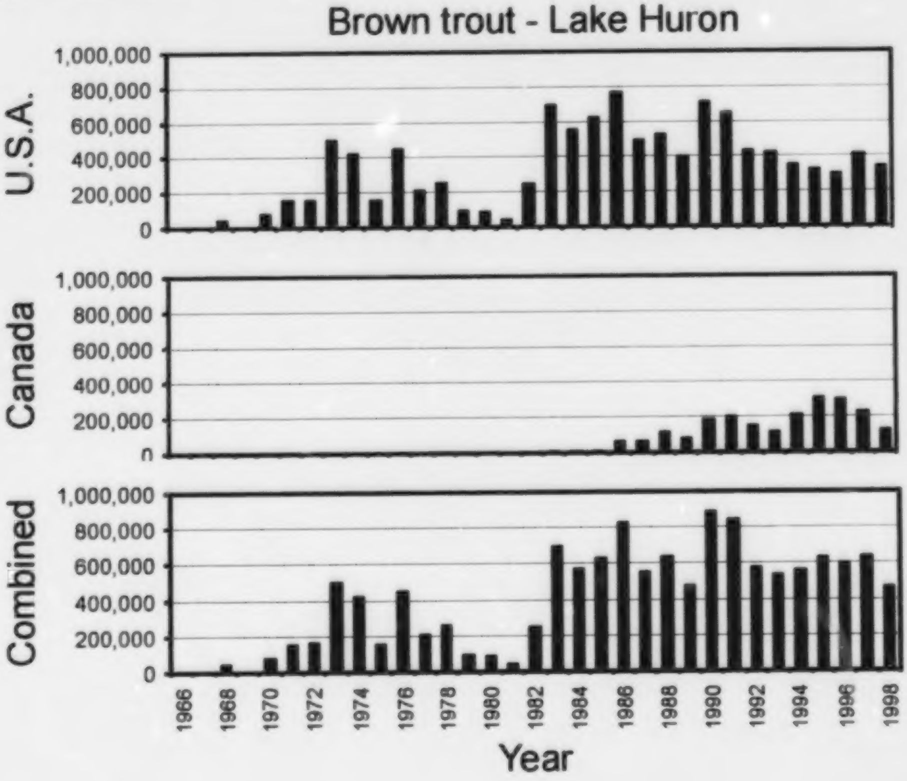
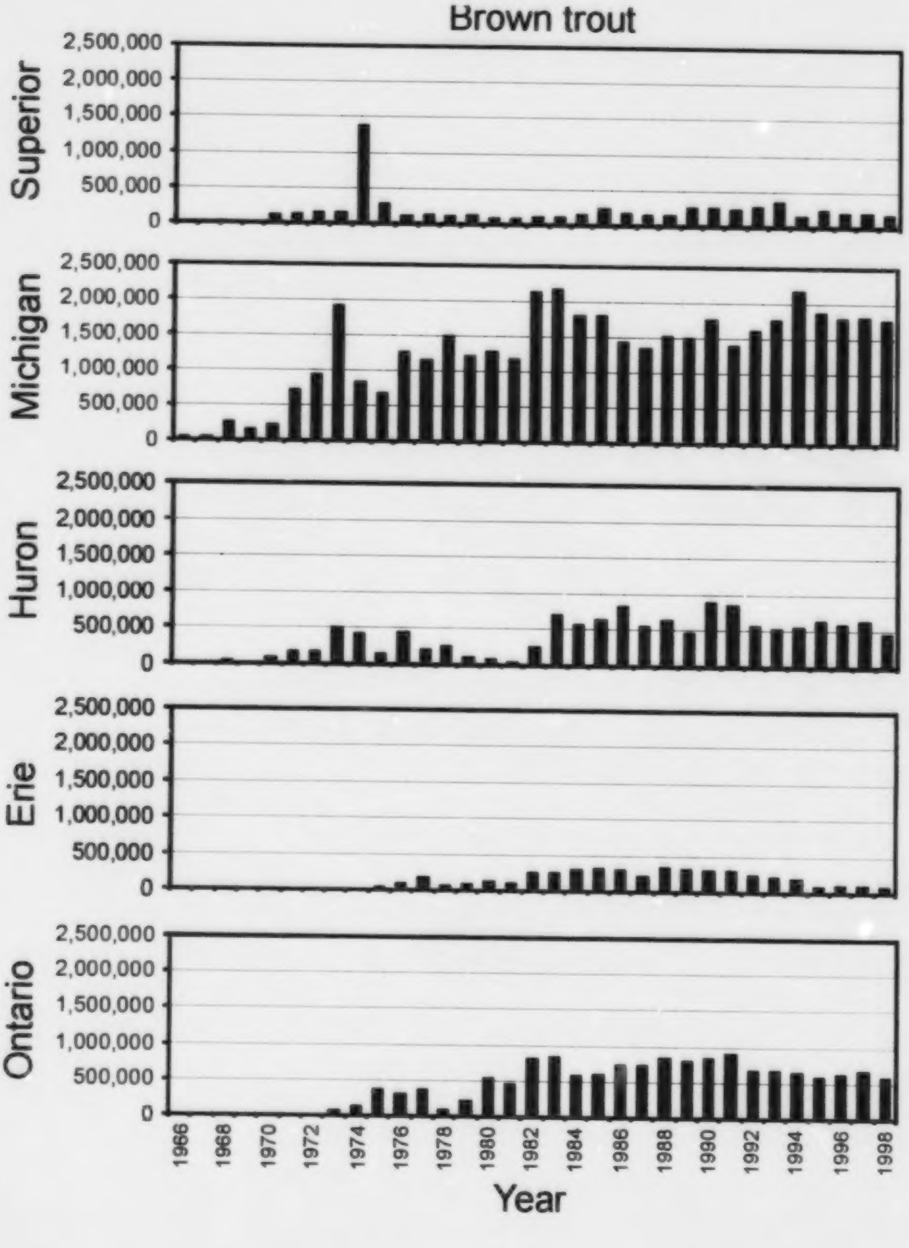


Fig. 19. Number of brown trout (*Salmo trutta*) stocked in each of the Laurentian Great Lakes for the period 1966–1998.



2.2 Pacific salmonines

2.2.1 Chinook salmon (*Oncorhynchus tshawytscha*)

The chinook salmon (Fig. 20) is native to the Pacific Ocean and its freshwater coastal tributaries from the Bering Sea southwest to northern Japan, and southeast to southern California (Hubbs and Lagler 1958; Scott and Crossman 1973).

Within six years of Samuel Wilmot constructing the 1866 Newcastle hatchery for re-stocking Atlantic salmon to Lake Ontario, the United States Commission of Fish and Fisheries had established a fisheries station on the Sacramento River (California). The sole purpose of this fisheries station was to collect, fertilize and distribute millions of eggs from Pacific salmonines for introduction elsewhere in North America and the world (Scott and Crossman 1973; MacCrimmon 1965, 1977).

The objectives for introducing Pacific salmon varied with species and location in the Great Lakes. Major reasons for their release were to (1) enhance the declining commercial food fisheries of the late 1800s (Mills et al. 1993), and (2) support a recreational fishery (MacKay 1969). In supporting food fisheries, the ultimate reason for the introductions was apparently to counter the effects of over-exploitation by European settlers of the native lake whitefish and lake charr populations, and to counter the deterioration of the fishes' food supply and habitat (Wilmot 1882).

In the autumn of 1873, both Wilmot and Seth Green — an American counterpart — hatched chinook salmon from the McLeod River (Sacramento River drainage basin, California) in their recently constructed facilities on tributaries to Lake Ontario (Huntsman and Dymond 1940; Parsons 1973; MacCrimmon 1977). In the spring of 1874, Wilmot released 68,000 chinook juveniles in Wilmot Creek below his hatchery; Green stocked chinook juveniles in U.S. tributaries of Lakes Ontario, Erie and Michigan. About the same time, the Ohio Fish Commission and the State of Michigan also began introducing thousands of chinook juveniles into Lakes Erie, Huron, Michigan and their tributaries (MacKay 1969; Mills et al. 1993).

Once again, Samuel Wilmot (1878) provided a fascinating, first-hand account of introducing chinook salmon — the California Salmon — in the Laurentian Great Lakes:

> *"The experiment of introducing and acclimatizing the salmon of the Pacific coast to the waters on this side of the continent, commenced at this establishment [Newcastle salmon hatchery] (kindly aided by Professors Baird and Mr. Livingstone Stone of the United States Fishery Commission) has been practically demonstrated by the fact that several of these salmon have been taken in Lake Ontario and in this stream (Wilmot's Creek) during last season.*
>
> *In October, 1873 the first ova of the California salmon (Salmo Quinnet) were brought over from the McLeod River. Twenty thousand of these were donated to this institution by Professor Baird. The eggs arrived safely and were hatched out in the following December. Many of the fry were let loose into this creek in April, 1874. In the fall of 1874, a second lot of these eggs were obtained from the United States hatchery on the McLeod River. The crop of fry from these proved most satisfactory. A large number of the young fish were put in Wilmot's Creek and at other points in the spring of 1875. A third consignment was received in October, 1875. The fry of those were distributed during the spring of 1876; some in the Saugeen River, others in some of the back lakes and the balance in the*

Fig. 20. Chinook salmon (*Oncorhynchus tshawytscha*) introduced to the Laurentian Great Lakes drainage basin. This specimen was angled in September 2000 during anadromous migration in the Nottawasaga River (Lake Huron basin). Photo credit: Chris Weland.

different streams. The fourth quota received in October, 1876, has already been referred to; I will now state that the success attending all these consignments of ova, both in their transportation, their hatching into fry and their distribution afterwards, was with the one exception of a remarkably satisfactory nature.

The assiduity practised in connection with this interesting venture met its reward in the face of 1876, by the capture of a veritable California salmon in Wilmot's Creek. Publicity was given to this fact and I here quote an extract from the annual report of 1876 in which mention is made of it. "It is well to make mention here (for it is the first record of the kind on this Atlantic side of the continent) that a California salmon was taken last autumn in this creek, in company with his Ontario cousins. This fish, following out the instinct of its species, must have migrated from Lake Ontario (some would say the Atlantic or Pacific Ocean) up this stream, for it was taken out of the trap in the reception house [of the Newcastle hatchery] along with other salmon that had entered it. The appearance at once indicated the salmo quinnet or California salmon; the length was fifteen inches, the body deep and narrow, with a deeply vermiculated greenish shade on the back inclining to brown towards the belly. The first lot of California eggs received at this place was in the fall of 1874; this salmon

> *must, therefore, have been two years old, from the egg, as it was taken in the month of October last. It was totally unlike the ordinary grilse or smolt of the stream; it was a male fish and had matured milt, The fact of this young Californian being taken here goes to show that it is not requisite that salmon should go to salt water to obtain their growth; and is also evidence in favour of the opinion advanced by me that the salmo salar (in like manner as the salmo quinnet) can be acclimated to and also be made natives of, our fresh water lakes."*
>
> *Further and more convincing proof of these fish becoming acclimatized to the fresh waters of Ontario is found in the fact of the netting of several of them in July last (1877) in Like Ontario. near the estuary of Wilmot's Creek; they were captured along with others of the native salmon of the country. One was a very beautifully developed specimen of upwards of five pounds in weight; its symmetry, though perfect, was different to the native salmon, its body was much deeper and more of the bass form; its flesh had changed from the deep red of the Pacific salmon to a whitish orange color; it was, however, wonderfully fat and extremely delicious for the table. The skin of this fish was preserved and mounted and is retained here as an interesting specimen of the first adult salmo quinnet taken on this side of the Pacific slope.*
>
> *Still further evidence is given of their naturalization here and of retaining their instinctive migratory habits, as several of these California salmon returned in September and October last to the hatching-house where they were reared, for the purposes of spawning. All of these were males and of fair size; one measured twenty-three inches in length. These fish were undoubtedly a portion of the first fry turned out from this nursery in the spring of 1874 and will be found to be the "advanced guard" or forerunners of others of their species that will show themselves next season.*
>
> *These salmon give interesting data for the naturalist and the study of physiology. They furthermore practically prove statements hitherto advanced by myself, that the salmon of the sea can be acclimatized and made natives of the fresh water lakes and that it is not indispensably requisite for salmon to go to salt water; large bodies of either salt or fresh water, with an abundant supply of food, is all that is requisite to give them growth and reproducing powers; and that the procreative qualities of the male salmon are usually developed at an earlier stage than the female, the former invariably commence their migration up the rivers for spawning purposes one year in advance of the latter; hence the indisputable fact of grilse taken in rivers being always males.*
>
> *A large number of eggs were gathered last October and November and placed in the breeding troughs of this nursery. The quantity obtained was not as great as that of the previous year, but this is accounted for by the salmon not coming as far up the stream as usual and having entered the creek some ten days later than formerly. Seven hundred and fifty thousand ova were gathered by the artificial methods and are now in a very healthy condition and are doing remarkably well and bid fair to yield a satisfactory percentage of fry."* (Wilmot 1878, p. 19)

The recovery of that first adult male chinook in Wilmot Creek was not only the first record of a Pacific salmon in eastern North America, it also provided proof (proudly announced by Wilmot) that the species could reach sexual maturity without access to sea. The first evidence of spawning by chinook in Lake Ontario tributaries came in the autumn of 1880 with a spent female; however, the Lake Ontario population ultimately never amounted to much (MacCrimmon 1977).

Subsequent plantings of chinook in Lake Superior rounded out coverage of early introductions to all of the Great Lakes (Parsons 1973; MacCrimmon 1977; Peck et al. 1999). Hundreds of thousands of chinook salmon continued to be released to each of the Great Lakes until approximately 1880 (Scott and Crossman 1973; MacCrimmon 1977). By 1880, numerous chinook salmon were being harvested by commercial fishermen in Lake Ontario — but almost entirely in Canadian waters and only in the general vicinity of Wilmot Creek (MacCrimmon 1977). Elsewhere, the returns from stocking efforts were not as high. Of the 500,000+ juvenile chinook salmon released into Lake Erie to 1880, only one recovery was reported in 1876; of the 250,000+ chinook salmon planted in the tributaries of Lakes Huron and Superior from 1874 to 1879, no recoveries were reported at all (MacCrimmon 1977). Gradually, even the Lake Ontario stock of chinook salmon disappeared altogether. In 1882, both American and Canadian plans to introduce chinook salmon to the Great Lakes were abandoned (Dymond et al. 1929; Peck et al. 1999).

In 1881, Samuel Wilmot wrote to S.F. Baird, an American ichthyologist from whom he had received his first shipment of chinook salmon for hatchery-rearing and introduction to the Great Lakes:

> *"... for consolation of [the loss of Atlantic salmon] I must only look forward to next year for a regular "Pacific coast" run of salmon and in such numbers as to crowd themselves upon the banks of the stream. In this idea I confess I have little or no faith, for I fear the production and growth in frontier streams of Ontario of the salmon and speckled trout [native brook charr]. This view has been forced upon me from the many experiments which I failed to carry out in the trials to restock ponds and streams (with brook trout) within short distances of their entrance to Lake Ontario. This state of things has been brought about by the almost total clearing up of the country causing many streams to become almost dried up in midsummer and all others to be greatly reduced in their volume of water. This very much lessened supply becomes overheated from the sun's rays and other atmospheric influences; add to this filth and decomposed matter of all kinds, carried by every rainfall into these streams from barn-yards, plowed fields, turnpike roads, sawmills and factories of all kinds; this so pollutes the water that the young of the higher orders of fish, such as salmon and trout, cannot live and thrive in such places."* (Wilmot 1882, p. 348)

Wilmot clearly recognized the relationship between early European activities in the Great Lakes region, the demise of the native salmonines and the probability of success for subsequent salmonine introductions.

After a period of respite following the initial stocking failures, the American states and Ontario began a new round of chinook introductions to the Great Lakes. In 1916, the Ontario government stocked 100,000 chinook embryos from the Fraser River (British Columbia) to Lake Ontario tributaries (MacCrimmon 1977). Annual plantings of similar magnitude continued until 1925 (Ricker and Loftus 1968). Unlike previous stocking attempts, there were numerous reports of chinook salmon returning to rivers by 1919, and the first reports of successful wild spawning in the Credit River and Twelve Mile Creek (Ontario) by 1927 (MacKay 1969; Scott and Crossman 1973; MacCrimmon 1977). Concurrently, American fisheries agencies resumed chinook salmon stocking, particularly in the tributaries of Lake Ontario; however, returns of the combined introduction efforts soon declined:

> *"United States plantings in Lake Ontario had been resumed in 1919, but, because of the opinion that nursery streams in New York State were no longer suitable for young fish, all of the hatchery-reared chinooks were released on various lake shoals known to be traditional spawning areas for the native lake trout. Whether or not these lake plantings contributed to the ephemeral build-up of chinooks in Canadian waters is unknown, but the second round of attempts to establish a Pacific salmon population in Lake Ontario was doomed despite early optimism."* (MacCrimmon 1977, p. 134)

Apparently, American fisheries managers considered the tributaries unfit to accommodate the requirements of the introduced chinook salmon. The suggestion that these waters were "no longer suitable for young fish" suggests not only the inappropriateness of these habitats for reproduction of this Pacific salmonine, but also that human agriculture, urbanization and industrialization had made the waters unfit for survival of fish in general.

The cumulative effects of the stocking programs to 1933 — estimates ranging from 9.3 to 11 million fish released (Kocik and Jones 1999; Peck et al. 1999, respectively) — could only be described as a dismal failure. Despite initial indications that the chinook salmon would thrive, particularly in Lake Ontario, the species failed to establish self-sustaining, permanent populations in the lakes and their tributaries (Crossman 1968; Scott and Crossman 1973; Emery 1985). The occasional chinook salmon was captured after the stocking programs ceased; however, by 1958, Hubbs and Lagler declared that this species was rare or extinct in the Great Lakes.

Near the beginning of the recent era of salmonine introductions to the Great Lakes, a chinook salmon stocking program in the freshwaters of the American Atlantic coast was undertaken.

> *"Establishing this voracious, fish-eating but non-reproducing species in the fresh waters of New Hampshire led to the interesting suggestion of using it in fresh water for control of coarse fish. The chinooks exterminated smelt from a lake in 3 years and then died out themselves, leaving the lake ready for the re-introduction of native trout."* (Scott and Crossman 1973, p. 176)

The salmon experience in New Hampshire apparently caught the attention of American fisheries biologists who were seeking management tools that would achieve two objectives: (1) decrease the abundance of non-native rainbow smelt and alewife in the Great Lakes and (2) establish recreational and commercial fisheries in waters where native salmonines (e.g., lake charr) were scarce or extinct.

Henry Regier (personal communication, 1997) recalls that Dr. A. Pritchard (then a Canadian GLFC Commissioner) chastised Michigan fisheries managers for proceeding without as much as a prospectus. In fact, a split in management objectives had already occurred between U.S. federal and state managers regarding the fundamental objectives for fisheries rehabilitation in the Great Lakes: federal officials supported the use of native lake charr, predominantly to support commercial fisheries; state officials supported the use of introduced salmonines, predominantly to support recreational fisheries (Tanner 2000).

In Tody and Tanner's (1966) salmonine introduction proposal, the only major reference to chinook salmon was as follows:

> *"Chinook salmon apparently have many characteristics that would qualify them for introduction to the upper Great Lakes. Chinooks have even lower stream and hatchery demands than do coho. They are much larger, have a more prolonged ocean or lake period of residence, and feed to a greater extent on a fish diet than coho. A freshwater strain has developed in New Zealand (Burstall, 1966, personal communication)."* (Tody and Tanner 1966, p. 4)

In spite of these 'desirable' characteristics, Tody and Tanner (1966) stated that chinook salmon introductions would be delayed until after initial coho salmon introductions, mostly due to greater technical difficulties in obtaining eggs and distributing hatchery-reared offspring.

In 1967, Michigan planted 800,000+ juvenile chinook salmon from Washington (Columbia River, Green River) in the Little Manistee and Muskegon rivers of Lake Michigan and the Big Huron River of Lake Superior (Parsons 1973; MacCrimmon 1977; Keller et al. 1989; Weeder 1997; Peck et al. 1999; but see Tanner 2000). Later, chinook salmon from Puget Sound were included in the hatchery programs (Keller et al. 1989). In 1969, abundant chinook salmon were the target of a new and explosive recreational fishery (Fig. 21) — catching over 100,000 chinook salmon in Lake Michigan alone (see McDowall 1978 for a similar explosion of introduced sport fishes in New Zealand). Within one year, the States of Michigan and New York were releasing 'astronomical' numbers of chinook salmon in American waters of Lakes Huron, Erie and Ontario (Scott and Crossman 1973; MacCrimmon 1977; Ebener 1995b). By 1977, all of the U.S. states were involved in chinook salmon stocking programs (Kocik and Jones 1999). Chinook salmon originating in American waters of Lakes Michigan and Huron soon migrated great distances, being captured in Ontario's Saugeen River (Lake Huron) and as far away as the Pelee region of Lake Erie (Crossman 1968; MacCrimmon 1977). Minnesota also introduced a spring-spawning strain of chinook salmon obtained from Idaho and Washington during the period 1974–1978 (Peck et al. 1999)

During the early era, chinook salmon introduced to the Great Lakes foraged extensively on abundant alewife and rainbow smelt, leading to extremely high growth rates (Crossman 1968; Scott and Crossman 1973). It is no wonder that many fisheries managers were enchanted with the results of the chinook salmon introductions; this species was satisfying objectives for recreational fisheries beyond their greatest expectations (Emery 1985).

In 1971, Ontario initiated its own chinook salmon stocking program for Canadian waters of Lakes Ontario and Superior (Appendix I). However, in contrast to the American experience, the Ontario stocking programs yielded 'negligible' returns to the recreational fishery (MacCrimmon 1977). As of 1977, there were apparently no spawning runs of chinook salmon in any Canadian rivers of either Lake Ontario or Lake Erie, and there were only weak runs of fish in Canadian rivers of Lakes Huron and Superior (MacCrimmon 1977). To this point, the Province of Ontario had not conducted any comprehensive assessment program to determine the progress of its chinook salmon stocking program:

> *"If it were not for the occasional harvests of chinooks from the open waters of Lakes Erie, Huron and Superior by Ontario commercial net fishermen, the wanderings of the species in Canadian waters would be but poorly documented. Whether or not the species is reproducing successfully in any of our Ontario streams is unknown, and it is impossible to know how long the chinook salmon*

Fig. 21. Recreational fishing for coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) on Lake Michigan during the late 1960s. Photo source: F.W.H. Beamish.

> *"The coho [and chinook salmon] is aimed at a specific fisheries management problem — namely to elevate the fisheries resource of the Great Lakes to its maximum potential for recreational fishing. The challenge in adapting the coho [and chinook salmon] to the fresh-water environment of the Great Lakes is an intriguing one. Nowhere in the world has the species been permanently established outside its native range in the North Pacific coastal area. Management objectives are even more challenging. The ultimate aim is to convert an estimated annual production of 200 million pounds of low value fishes — mainly alewives — that now teem in the upper Great Lakes into an abundance of sport fishes for the recreational fishermen."* (Tody and Tanner 1966, p. 1)

> *would be self-sustaining in the Great Lakes basin should the massive plantings by United States agencies be dismissed."* (MacCrimmon 1977, p. 134)

Apparently, the Canadian attempts to establish chinook salmon populations in the Great Lakes were relatively unsuccessful, compared to the programs conducted by the American fisheries agencies. Under authority of the Ontario Ministry of Natural Resources, angler groups in Ontario began rearing chinook salmon in private hatcheries and releasing them into Lake Huron beginning in 1985, and in Lake Superior beginning in 1988 (Kocik and Jones 1999).

It should be noted that in the 1980s, angler interest focussed on the possibility of introducing a new, artificially-created form of this species known as the 'super-chinook' (Toronto Star 1986). This form could be created in hatcheries by heat- or chemical-treatment of eggs during early development, leading to sterile adults that exceeded 25 kg (55 pounds) by eating even more forage fish than the 'normal' strains of chinook salmon introduced to the Great Lakes (OMNR 1987):

> *"The state of Wisconsin stocked 80 000 sterilized chinook salmon (*Oncorhynchus tshawytscha*) in Lake Michigan during the spring of 1986 and intends to stock 100 000 sterilized chinook salmon annually (M. Hansen, Wisconsin Department of Natural Resources, Madison, WI, pers. comm.). The state of Michigan plans a similar program (Husar 1985) and initiated it by stocking approximately 25 000 sterile chinook in 1986)."* (Kitchell and Hewett 1987, p. 384)

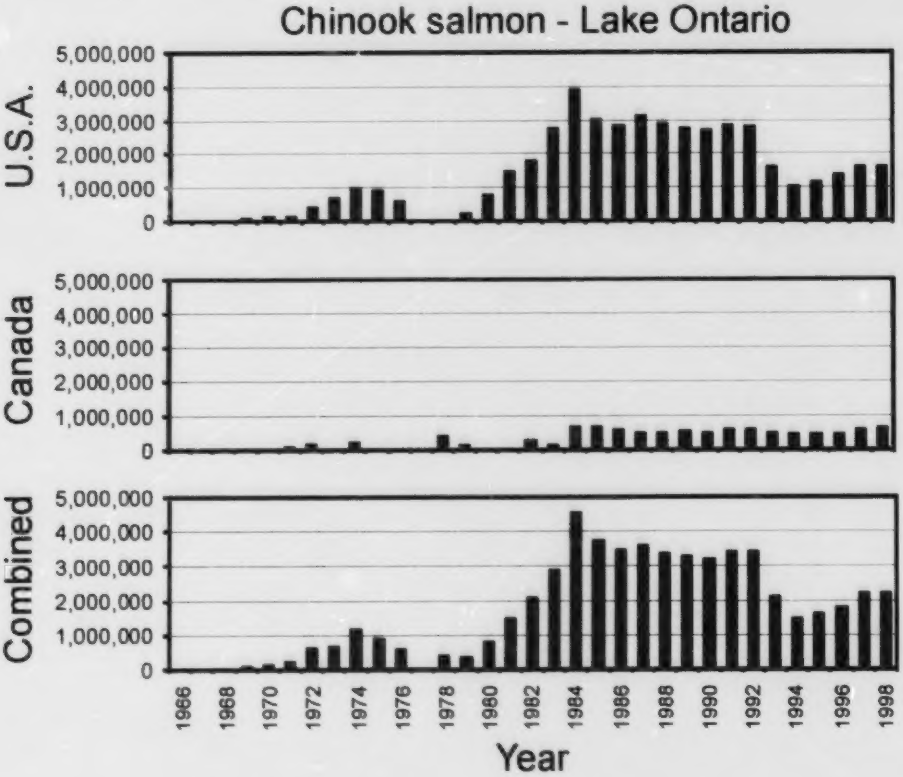
These sterilized chinook salmon did not divert much energy to reproduction (e.g., gonads, migration, spawning), but rather exhibited elevated growth rates, thus contributing to a population of larger trophy fish for the recreational fisheries (Kitchell and Hewett 1987).

During the period 1966–1998, an astounding 336 million chinook salmon were introduced to the Great Lakes ecosystem (Appendix I). In contrast to popular opinion, Lake Ontario accounted for less than 20% of the total chinook salmon stocking — and this was almost entirely associated with releases from American hatcheries (Fig. 22). Lake Huron (Fig. 23) and Lake Superior (Fig. 24) experienced intermediate levels of chinook stocking from 1966 to 1998; 'intermediate' in comparison to the staggering 153 million chinook salmon (45% of total) released into Lake Michigan during the same period (Fig. 25). Taken as a whole, more than 92% of all chinook salmon introduced to the Great Lakes ecosystem in the modern era have been released by American hatcheries.

Once released, chinook salmon have been reported to move extensively within, and between, Great Lakes basins (e.g., LHMU 1998; Peck et al. 1999). Carl (1982) estimated that approximately 23% of Lake Michigan chinook salmon originated from wild reproduction in Michigan tributaries (see also Weeder 1997). Elliott (1994) estimated that wild production accounted for 45–66% of chinook salmon populations in the northeast basin of Lake Michigan and 27–37% in the southeast basin. Hesse (1994) suggested that chinook salmon had become 'naturalized' in eastern Lake Michigan, based on an estimated 30% contribution of wild recruits to the harvested population(s). Peck et al. (1994, 1999) reported that chinook salmon from wild reproduction constituted 50–90% of the harvest sampled across most of Lake Superior in 1989–1994.

In contrast, relatively low contributions from wild reproduction have been reported elsewhere in Lakes Superior, Huron and Ontario (Berg 1978; Johnson 1978; Borgeson 1981; Johnson and Ringler 1981). In Lake Michigan, numbers of spawning chinook returning to tributaries began to decline about 1985, and by 1988 were estimated to be 40–50% lower than in the early 1980's (Stewart and Ibarra 1991). Other studies have shown that some chinook salmon populations were almost entirely dependent on the release of hatchery-reared juveniles (e.g., Avery 1974; Patriarche 1980; Emery 1985). Despite reports of self-sustaining wild reproduction of chinook salmon (e.g., Jones and Schreiner 1997 in Negus 1999; Hesse 1994; Bence and Smith 1999; Eshenroder and Burnham-Curtis 1999; Peck et al. 1999), it is not clear that this species would persist in the Great Lakes without the support of ongoing stocking programs.

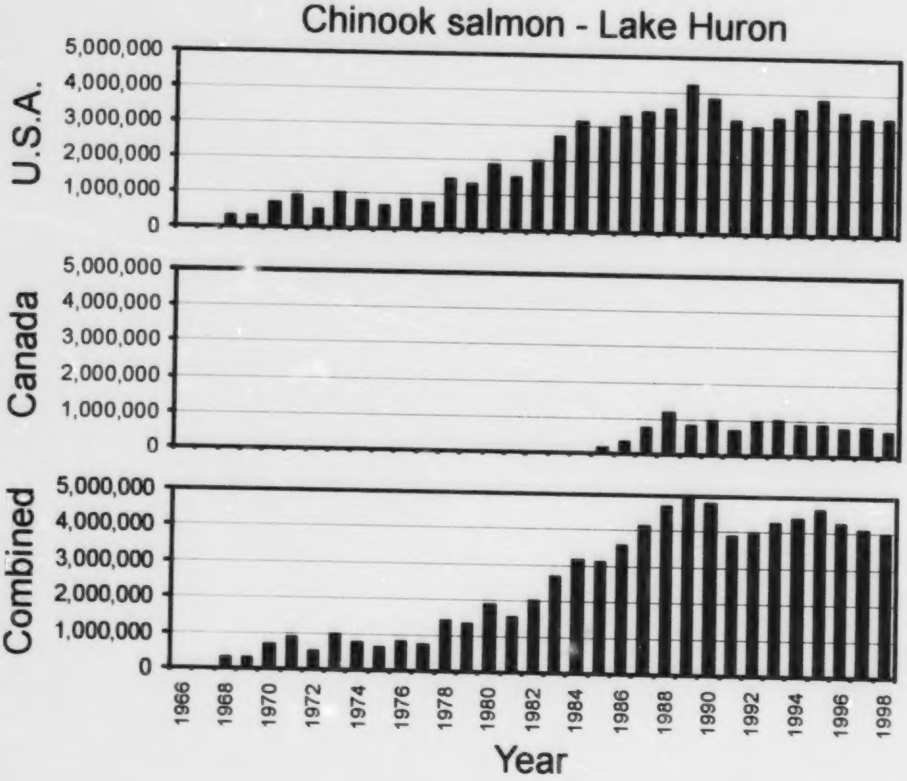
Fig. 22. Number of chinook salmon (*Oncorhynchus tshawytscha*) stocked by jurisdiction in Lake Ontario for the period 1966–1998.



Beginning in 1987, chinook salmon in Lake Michigan began to show the consequences of overstocking. Lakewide chinook salmon harvest and catch-per-unit-effort (taken as a relative measure of abundance) began to decline dramatically (Keller et al. 1989; Stewart and Ibarra 1991). In 1988/89, massive mortalities of chinook salmon were observed in the southern end of Lake Michigan (Nelson and Hnath 1990):

> *"...management focus shifted abruptly in the late 1980s when large chinook salmon began dying from bacterial kidney disease (BKD) in southern Lake Michigan (Stewart and Ibarra 1991). Some thought this was a fish disease problem that could be solved by improving hatchery practices, whereas others thought this was a prey deficit problem, with BKD expressing itself only because the chinook salmon were severely stressed by a lack of alewife food. The apparent dilemma for managers was: do we stock more chinook salmon to offset the higher BKD-induced mortality, or do we stock less to alleviate the potential for nutritionally-induced stress? The management rationale is not documented, but some agencies reduced the number of chinook salmon*

Fig. 23. Number of chinook salmon (*Oncorhynchus tshawytscha*) stocked by jurisdiction in Lake Huron for the period 1966–1998.



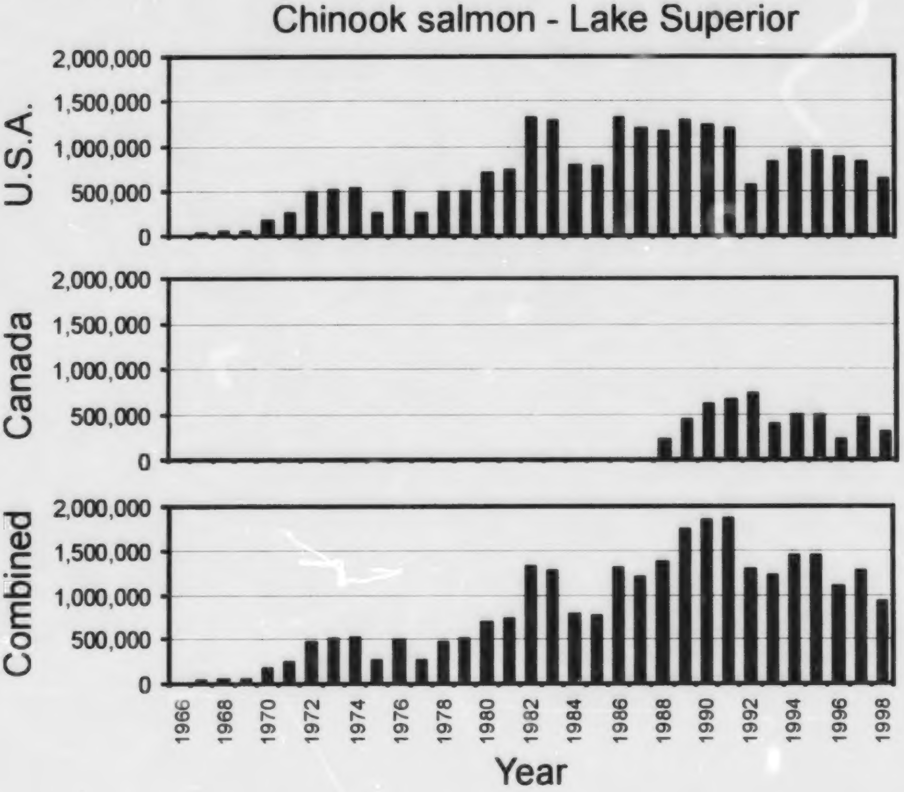
> *released, whereas other agencies increased the number released, with the result being that the total number of chinook salmon planted rose to its highest level in 1989 (Kocik and Jones 1999). Despite enhanced stocking, by 1993, the number of chinook salmon harvested by anglers had declined to a small fraction of former levels in all the states bordering Lake Michigan (Bence and Smith 1999).*" (O'Gorman and Stewart 1999, p. 504, their emphasis)

After clinical diagnostics had been undertaken, fisheries managers accepted the fact that they had exceeded the carrying capacity of Lake Michigan so badly that they had triggered an epidemic of bacterial kidney disease (BKD) — one of nature's density-dependent ways of saying there were far too many hatchery fish in the ecosystem.

The recent history of Great Lakes chinook salmon fisheries is plagued with more consequences of overstocking. Consider this account of circumstances in Lake Ontario:

> "*The last several years have brought changes that could potentially have important consequences to the sport fishery in the near future. By 1990, the*

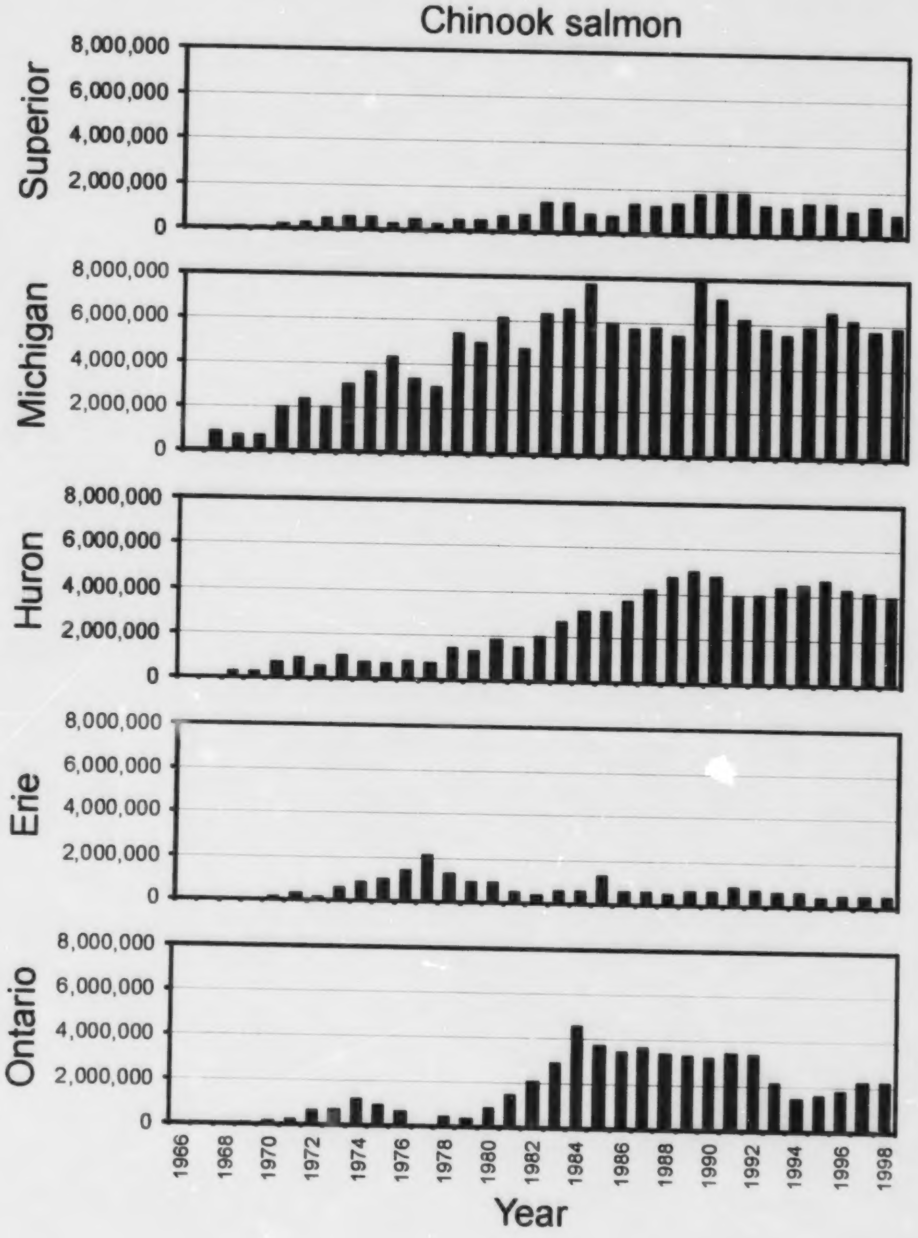
Fig. 24. Number of chinook salmon (*Oncorhynchus tshawytscha*) stocked by jurisdiction in Lake Superior for the period 1966–1998.



> *stocking rate of salmonines in Lake Ontario was the highest per unit area of any of the Great Lakes, while natural productivity of the forage base was thought to be decreasing due to reversal of cultural eutrophication and invasion of the zebra mussel (Jones et al. 1993; Lange et al. 1995). Simulation modeling suggested that the salmonine fishery in Lake Ontario might be sensitive to a die-off of alewives following a severe winter (Jones et al. 1993). In response to these concerns and observations of a collapse of the chinook salmon fishery in Lake Michigan, New York, and Ontario agreed to substantially reduce salmonine stocking rates starting in 1993, primarily by reducing numbers of chinook salmon and lake trout planted (Orsatti and LeTendre 1994; Lange et al. 1995). Lakewide stocking was reduced from 8 million to 5 million salmonines in 1993, and further reduced to 4.5 million in 1994." (Bence and Smith 1999, p. 292)*

Notwithstanding conceptual problems with these eutrophication and mussel hypotheses, the Lake Ontario example serves to underscore the magnitude of demand for chinook salmon by the recreational fisheries — in relation to the maximum carrying capacity of the Great Lakes.

Fig. 25. Number of chinook salmon (*Oncorhynchus tshawytscha*) stocked in each of the Laurentian Great Lakes for the period 1966–1998.



2.2.2 Coho salmon (*Oncorhynchus kisutch*)

The coho salmon (Fig. 26) is a species which is native to the Pacific Ocean and its tributaries from Alaska southeast to northern California, and southwest to Japan (Scott and Crossman 1973).

According to Scott and Crossman (1973), the first attempt to introduce coho salmon to the Great Lakes drainage basin occurred in the 1870's when government hatcheries in Ontario, Ohio and Michigan released thousands of juveniles into Lake Erie and its tributaries. Although there is little documentation of this introduction, it likely was intended to support a commercial or recreational fishery. These coho salmon did not establish spawning populations, and the stocking programs were terminated. Mills et al. (1993) made a vague reference to the possibility that coho salmon may also have been accidentally released into the Great Lakes; however, they provided no further details.

In 1933, the Ohio Department of Conservation introduced 41,000 coho salmon to two tributaries of Lake Erie (Parsons 1973; Emery 1985; Kocik and Jones 1999). Some degree of wild reproduction apparently resulted from this stocking program; however, no self-sustaining populations were established (Scott and Crossman 1973; Mills et al. 1993). This second round of stocking coho salmon in the Great Lakes was terminated in 1935.

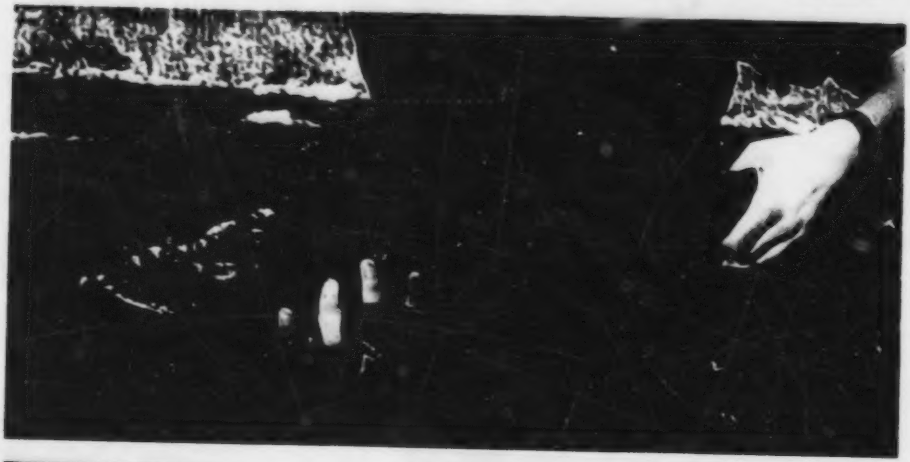
A coho salmon introduction program was re-initiated in the Great Lakes by the States of Michigan and Ohio in the mid-1960s (Parsons 1973). For the first time in the modern history of Great Lakes fisheries management, a 1966 report by Drs. Wayne Tody and Howard Tanner gave an explicit description of the rationale employed by the fisheries managers, in this case the State of Michigan, for their salmonine introduction:

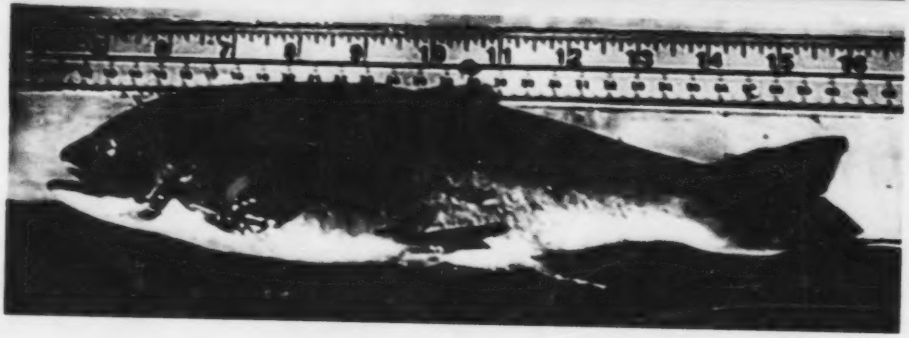
> *"Here then is a key to the future management of the fishery and a possible solution to the alewife problem. Namely, to increase, through management, the upstream runs of predacious fish like steelhead which will enter the Great Lakes at a size large enough to consume alewife. Along with the existing species [i.e., steelhead] we should introduce new species of equal value that can be brought to an even greater level of abundance. In addition we should, as necessary, undertake hatchery propagation to supplement natural reproduction. The goal must be to build a predator fish population of sufficient magnitude to utilize to the greatest possible degree the alewife and other low value species as forage. Maximum advantage can be derived through selection and propagation of game fish with the highest sporting qualities to support a recreational fishery. If they occur, surplus stocks can and should be harvested by the commercial fishery."* (Tody and Tanner 1966, p. 3, their underline)

Never before had the reasons for introducing non-native salmonines to the Great Lakes been so clearly stated. Not only were Michigan fisheries managers explicit about their objectives for the salmonine introduction program, they were also confidently optimistic:

> *"We were totally convinced that the introduction of salmon into the Great Lakes would succeed. Several examples in the literature described the successful introductions of salmon into freshwater that had succeeded, but on a small scale. The food supply represented by the billions of pounds of alewives was basic to our optimism."* (Tanner 2000, p. s13)

Fig. 26. Coho salmon (*Oncorhynchus kisutch*) introduced to the Laurentian Great Lakes drainage basin. *Top photo*: Sexually mature, male coho salmon sampled from a spawning migration up the Credit River (Lake Ontario basin) in November 2000. *Bottom photo*: 28.5 cm (precocious), sexually mature, male coho salmon sampled from a spawning migration up the Credit River (Lake Ontario basin) in November 2000. Photo credits: Bob Scott.





Apparently, the State of Michigan intended to satisfy its objectives by maximizing predator populations through hatchery releases above and beyond any wild reproduction that might occur. Such a maximization of salmon abundance would be achieved by channelling the conversion of alewife and other 'low value' forage species into species that would support the recreational fisheries. This interpretation is supported by a unique historical commentary presented by Kocik and Jones (1999):

> "*During the modern period [1966–present], management of the Great Lakes changed dramatically as U.S. states and Ontario began to take a more active role. To understand these decisions in their mid-1960's context, we consulted Dr. Howard Tanner, who was then Chief of Fisheries in Michigan. Dr. Tanner stated that two influential policy changes occurred at this time. First, Michigan decided to more actively manage its share of Great Lakes waters. Prior to this decision, federal agencies were responsible for most management activities*

> *occurring in Great Lakes waters. Secondly, state management emphasis was focussed upon enhancing Great Lakes sportfishing opportunities. The ensuing management goal was to introduce a popular game fish well suited to Great Lakes waters. Concurrent increases in Pacific Northwest coho and chinook salmon abundance provided an opportunity for Michigan to import eggs of these popular game fish. These introductions created popular sportfishing opportunities, and other states and Ontario soon followed suit."* (Kocik and Jones 1999, p. 457)

As mentioned in the preceding discussion of chinook salmon introductions, U.S. federal officials supported the use of native lake charr, predominantly to support commercial fisheries; state officials supported the use of introduced salmonines, predominantly to support recreational fisheries (Tanner 2000).

Not only did Tody and Tanner (1966) present the first comprehensive documentation of objectives and rationale for a non-native salmonine introduction to the Great Lakes, they also:

- reviewed the life-history characteristics of this species in its native range,
- discussed the potential adaptability of coho salmon to fresh water,
- presented the plan for introduction, including release schedules, locations and stocks.

In general, this was a relatively comprehensive and well-organized proposal. The report lacked only one major component — Tody and Tanner (1966) virtually ignored the need to evaluate other ecological effects of the proposed coho salmon introduction. The few statements that they did make regarding the need for ecological assessment of the introduction, were specifically concerned with the degree of success of the coho salmon stocking program, rather than its effects on the native community in the Great Lakes ecosystem. For example:

> *"Personnel and facilities will be required to follow the movements, distribution, rate of growth and food habits of the coho throughout the period of Great Lakes life. Inter-specific relationships and factors influencing mortality of the coho should be closely observed as well."* (Tody and Tanner 1966, p. 21)

Nothing more was said about the need for ecological evaluations or the methods by which such assessments should be undertaken. The reason for Tody and Tanner's (1966) omission of ecological assessment is not clear; however, it may be related to a fundamental assumption made by the authors:

> *"There is no chance that the coho could under any circumstances become an undesirable species such as the common carp. Any problems that may be encountered in the introduction of coho to Great Lakes waters will almost certainly be concerned with the difficulties of establishing this species to the level of abundance that the environment and demand by our people will require."* (Tody and Tanner 1966, p. 8)

Support for the modern coho salmon introduction program was not unanimous. Even before the State of Michigan released its first fish in this program, it was receiving criticism on the likelihood of negative ecological consequences:

> *"The decision by Michigan authorities to release coho salmon in Great Lakes waters was met with enthusiasm by some scientists and fishermen, but with*

> *skepticism by others. Still others condemned the idea of introducing yet another exotic fish of unproven merit and one which might cause irreparable damage to the indigenous Great Lakes fauna. Of no small concern was the possibility of adverse effects on brook, brown, and rainbow trout whose river spawning areas would be invaded each autumn by massive coho intent on breeding there. Despite the reservations which came from many sources, including Ontario, the State of Michigan proceeded with the implementation of its coho stocking plan."* (MacCrimmon 1977, p. 137)

> *"Both [kokanee and coho salmon] were earmarked for subsequent releases into Great Lakes waters amid dissenting views on the desirability of introducing such potentially prolific exotics without any knowledge of their likely impact on native fauna."* (MacCrimmon 1977, p. 142)

Opponents of this introduction were concerned with negative effects on "brook, brown, and rainbow trout" as if all were native Great Lakes species. It is somewhat ironic that a couple of non-native salmonines would require protection from the effects of another non-native salmonine (see McDowall 1978; 1994 for a New Zealand perspective on this issue).

In 1964, the State of Michigan obtained 1 million coho salmon embryos (Columbia River and Cascade River in Oregon) from the Oregon Fish Commission (Tanner 2000), of which 850,000 were reared to a juvenile state in hatcheries (Keller et al. 1989). In the spring of 1966, these juveniles were released into the Little Manistee and Muskegon Rivers of Lake Michigan, the Big Huron River of Lake Superior, as well as other Michigan tributaries to Lakes Superior and Huron (Scott and Crossman 1973; MacCrimmon 1977; Appendix I). Mills et al. (1993) also stated that Ohio released coho salmon in 1966; however, if this did occur, it was likely small in comparison to the efforts of Michigan. Later, coho salmon from the Toutle River in Washington State, and others from Alaska were also included in the introduction programs (Keller et al. 1989; Tanner 2000).

Unlike previous attempts to introduce coho salmon to the Great Lakes, the initial return from these plantings was described as immediate and spectacular (Crossman 1968; Aron and Smith 1971). The coho salmon apparently fed very effectively on the abundant alewife (Harney and Norden 1972); by the autumn of 1966, commercial and recreational fishermen in Lake Michigan were capturing numerous coho salmon (see also Fig. 21):

> *"The enthusiasm toward, and success of this introduction led to flotillas of angler's boats as small as canoes up to a mile offshore in the two lakes, and to a near catastrophe in a storm. This hoped for success with a new Great Lakes sport and commercial fish is not without its minor tragedies though. Thirty tons of spawning cohos were seined from one stream in one day, when officials became fearful of the results of mass die-off. These seined fish were sold to commercial fishermen who resold them to the public. Popular at first the market soon died as a result of dissatisfaction with their condition and quality."* (Crossman 1968, p. 11)

The transfer of coho biomass up the tributaries during spawning runs would likely have had severe effects on the riverine ecosystems (see Section 3.2.6); however, this phenomenon was apparently not the subject of study.

Biologists were astounded with the extremely fast growth rates for these fish, especially those in Lake Michigan (MacCrimmon 1977):

> *"It is obvious [from an examination of its diverse diet composition] why it was hoped coho in the Great Lakes would utilize the very abundant rainbow smelt and alewife. This they have done as these two species make up the bulk of the food of larger cohos taken."* (Scott and Crossman 1973, p. 162)

Some of the coho salmon that had migrated upriver in the autumn of 1966 were sexually mature, and biologists found coho salmon embryos in these tributaries — lending support to the idea that this species could complete a life cycle entirely in freshwater (MacCrimmon 1977).

In the spring and summer of 1967, Lake Michigan coho salmon dispersed widely, with Canadian anglers catching adults in Georgian Bay, Lake Huron and Lake Erie (Crossman 1968; Scott and Crossman 1973). The abundance of coho salmon continued to increase during the autumn runs of each year from 1967 to 1969. At this time, Ontario anglers were catching strays from the Michigan coho releases, while Ontario commercial fishermen were catching and selling up to 10,000 pounds of coho salmon from Michigan annually — despite the fact that Michigan commercial fishermen were prohibited from doing the same (Scott and Crossman 1973).

It was not long until other fisheries managers were implementing their own coho salmon introduction programs:

> *"In the face of such spectacular success from the initial coho plantings, other Great Lakes agencies could not resist the urge to follow Michigan's lead in salmon culture. In 1967, over a million eggs taken from returning parents were distributed to agencies in Wisconsin, Ohio, Pennsylvania, New York and Ontario. From that time onward, populations of coho salmon in the Great Lakes expanded as a result of both hatchery releases and the straying of mature fish into unfamiliar rivers where new spawning populations became rooted. By the fall of 1968 the species was reported from all of the Great Lakes, but least in Lake Ontario."* (MacCrimmon 1977, p. 138)

The Province of Ontario initially restricted coho introductions to Lake Ontario:

> *"Ontario biologists were slow, if not reluctant to join the coho bandwagon. With the exception of token plantings in streams on Nipigon Bay of Lake Superior between 1969 and 1971, the Province decided to restrict releases of coho salmon to the Lake Ontario watershed. Choosing three of the last streams from which the native Ontario salmon had disappeared nearly a century ago, plantings totalling 130,000 yearling fish were made in Bronte Creek and the Humber and Credit Rivers near Toronto during the spring of 1970. Special attention was paid to the Credit River where some seventy per cent of the hatchery-reared fish were placed."* (MacCrimmon 1977, p. 138)

Unfortunately, MacCrimmon (1977) did not elaborate on the reasons for Ontario's initial reluctance to stock coho salmon. It may be useful to recall that active and economically-successful commercial fisheries for smelt existed in Lake Erie (MacCallum and Regier 1970; Leach and Nepszy 1976), Lake Ontario (Christie 1972), Lake Michigan (Brown et al. 1999) and in Lake Superior (MacCallum and Selgeby 1987). This irony is only exaggerated when one considers the alewife commercial fisheries that also had to be closed down to protect the forage base of the introduced salmonines (see Brown et al. 1999; O'Gorman and Stewart 1999). These observations raise the question: was there really a need for biological control by introduced salmonines, when conventional harvesting was perceived as such a competitive threat to the stocking program?

At any rate, the initial results of Ontario coho salmon plantings were disappointing compared to those associated with Lake Michigan stocking efforts (Bence and Smith 1999); the returning spawners were fewer in number and smaller than their American counterparts. To date, there appear to have been few Ontario tributaries to the Great Lakes (e.g., Saugeen River — Lake Huron; Fisher's Creek — Lake Erie; Credit River — Lake Ontario; MacCrimmon 1977) that might support even a modest coho salmon population.

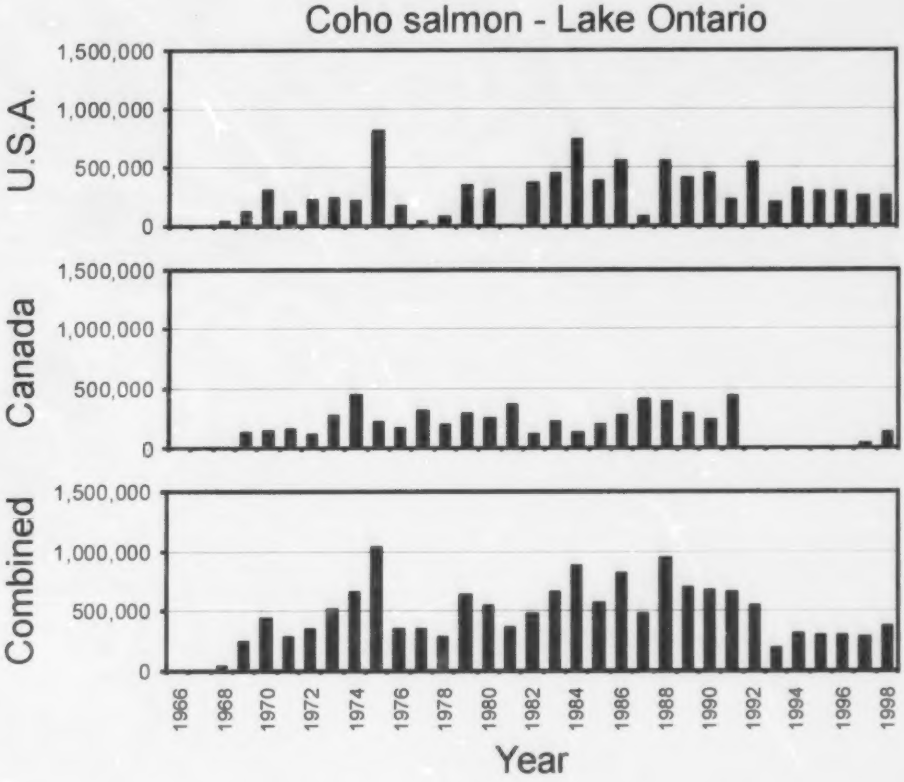
During the 3-year period 1966 to 1969, more than 10 million coho salmon were stocked in Great Lakes waters (Appendix I), of which approximately 2 million were captured later — mostly by recreational anglers (Parsons 1973). Coho salmon were obtained from the Columbia River (Washington) and released into Michigan tributaries of Lake Superior during 1967–1968; these fish were subsequently found to stray to several other streams in the basin (Peck 1970). Since then, millions of coho salmon have been released annually by both American and Canadian governments, and more recently by private sportsmen's groups (Ford 1997).

From 1966 to 1998, a total of more than 148 million coho salmon have been introduced to the Great Lake ecosystem (Appendix I). In Lake Ontario, coho salmon stocking was relatively light during the modern era (approximately 15 million or 10% of Great Lakes total), with a general balance between American and Canadian releases (Fig. 27). Lake Erie received approximately twice the stocking of coho salmon as for Lake Ontario, and all of these fish came from American hatcheries (Appendix I). In relative terms, Lake Huron and Lake Superior were 'lightly' stocked with coho salmon during the modern era (9–12 million fish per year); in these cases all (or virtually all) of the fish came from American hatcheries (Fig. 28, Appendix I). Once again, when viewed across the Great Lakes, it can be seen that more than half of all 148 million coho salmon releases have occurred in Lake Michigan — stocking in the other lakes has been light and variable, with a tendency for programs to fade out over the 1990s (Fig. 29). Taken as a whole, more than 95% of all coho salmon introduced to the Great Lakes ecosystem in the modern era have been released by American hatcheries.

Generally, it is considered that Great Lakes populations of coho salmon require annual stocking for their continued existence in the basin (Carl 1983; Emery 1985). Although large spawning runs of coho salmon have been reported in many Great Lakes tributaries (e.g., Peck 1970; Carl 1982), and there have been reports of substantial wild reproduction (e.g., Jones and Schreiner 1997 in Negus 1999; Marcogliese and Casselman 1998; Bence and Smith 1999), the actual extent of such reproduction has rarely been measured. In Lake Superior, investigators have recently begun to question the ability of ecological productivity to meet the demands of the hatchery stocking programs:

> *"Since their introduction to the Great Lakes in the 1960s, coho salmon have supported commercial and recreational fisheries in Lake Superior. Although the persistence of populations in this drainage has relied upon intensive and continued stocking, several tributaries to Lake Superior, especially near Chequamagon Bay (Wisconsin), are sources of natural reproduction (Becker 1983). Recently, declines in recreational harvests have raised questions about*

Fig. 27. Number of coho salmon (*Oncorhynchus kisutch*) stocked by jurisdiction in Lake Ontario for the period 1966–1998.



the factors that limit the natural reproduction of coho salmon populations in this region." (Ford and Lonzarich 2000, p. 94)

Interestingly, there has been a dramatic decline in coho salmon harvest in the Main Basin of Lake Huron since 1988; a decline which has been attributed to the cessation of stocking (Bence and Smith 1999). At least in some cases, it would appear that the potential for coho salmon to maintain wild populations in the Great Lakes is highly questionable.

Fig. 28. Number of coho salmon (*Oncorhynchus kisutch*) stocked by jurisdiction in Lake Superior for the period 1966–1998.

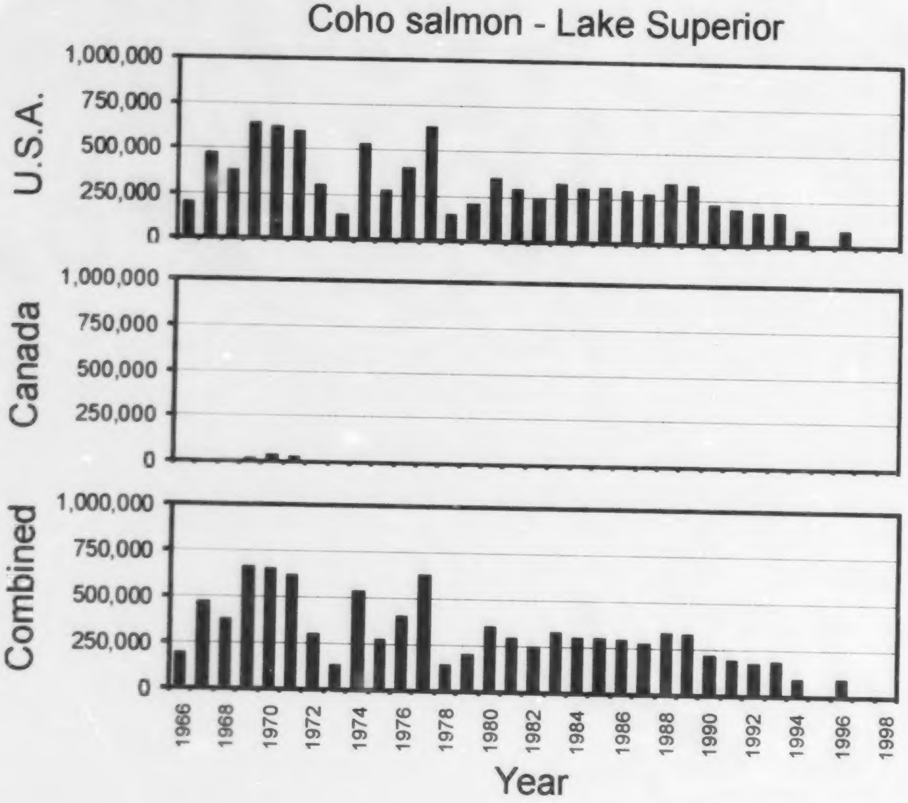
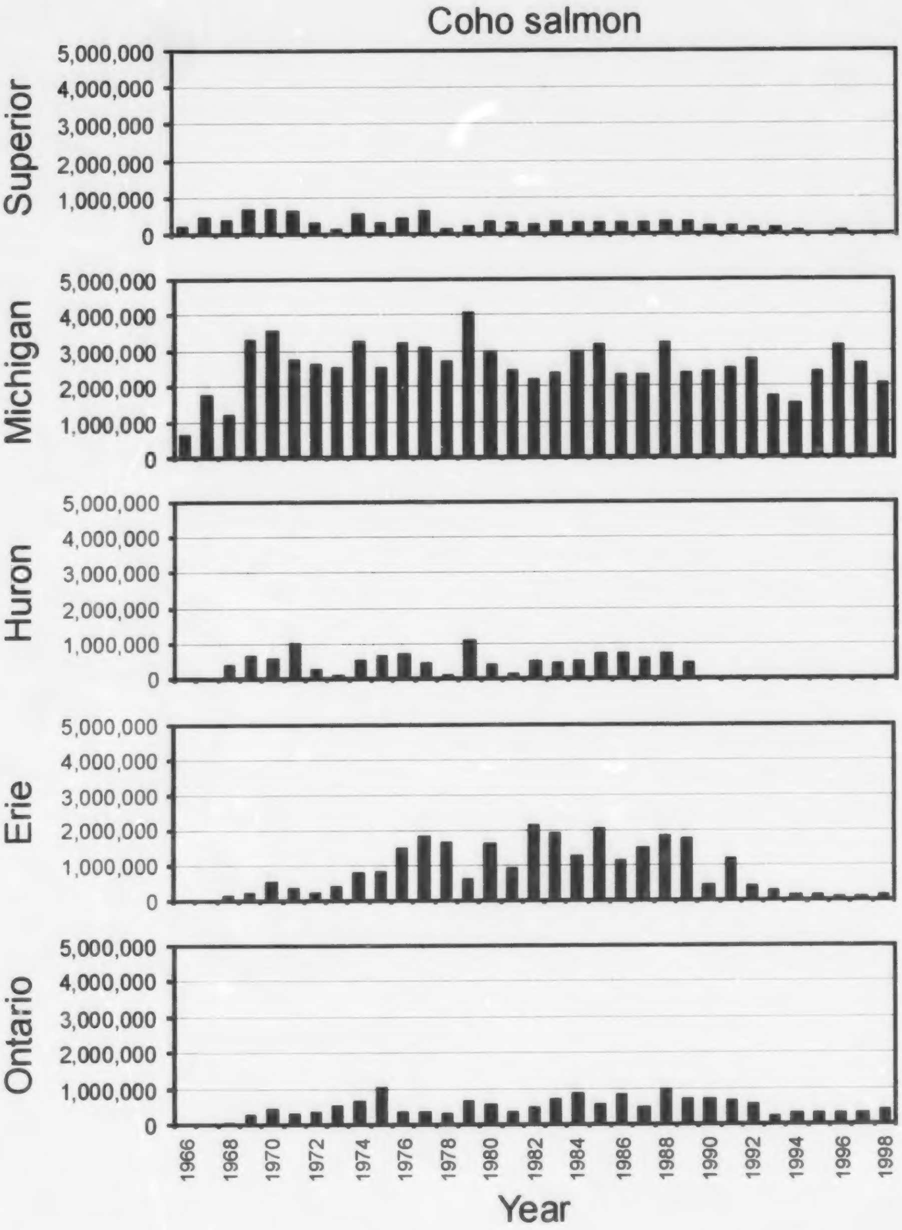


Fig. 29. Number of coho salmon (*Oncorhynchus kisutch*) stocked in each of the Laurentian Great Lakes for the period 1966–1998.



2.2.3 Rainbow trout (*Oncorhynchus mykiss*)

Contrary to a common misconception, the rainbow trout (Fig. 30) is *not* native to the Great Lakes. It is a member of the salmonine complex that is native to the eastern Pacific Ocean and freshwater tributaries from southern Alaska to southern California (Hubbs and Lagler 1958; Scott and Crossman 1973). Europeans first learned of the rainbow trout, along with the other Pacific salmonines, during their exploration of western North America:

> *"Ever since its first discovery amid the unspoiled wilderness of the Columbia River during the Lewis and Clark expedition of 1806, this comely salmonid has been valued by generations of anglers as one of the most fabulous of all sport fishes. Thus it was only natural that it should be transferred at an early date from its native haunts along the Pacific coast of North America to fishing waters in many parts of the world, including the Great Lakes basin."* (MacCrimmon 1977, p. 99)

From the outset, Europeans placed a high value on the rainbow trout as a desirable species that would support a strong recreational fishery (see also Bence and Smith 1999). Reference to the introduction of such a species outside of its native range as "*only natural*" is an ironic, if not wry, choice of words.

It should be noted that the rainbow trout was classified in 1836 as a member of the Atlantic salmonine genus *Salmo*; it has since been reclassified as belonging to the complex of Pacific salmons in the genus *Oncorhynchus* (Smith and Stearley 1989).

The rainbow trout demonstrates a phenomenal range of life-history characteristics in its native range (Scott and Crossman 1973). It is important to distinguish between two forms of this species:

- rainbow trout: a small and darkly coloured form, typically inhabiting fresh water rivers and streams
- steelhead: a larger, silvery form, typically inhabiting large open waterbodies (marine or freshwater).

In the Great Lakes, steelhead are distinguished from rainbow trout by their parr–smolt transformations and their subsequent migratory behaviour (Rand et al. 1993; Negus 1999). In this report, 'rainbow trout' will refer to the species rather than any particular form of the species. The form of 'rainbow trout' commonly recognised for its migratory behaviour (anadromous or 'potamodromous,' see Kocik and Jones 1999), will be identified as 'steelhead,' where appropriate.

Non-migratory rainbow trout were introduced to the Great Lakes drainage basin, along with chinook salmon (see above), during the early days of pioneer hatchery programs (Fig. 12):

> *"The introduction of the rainbow trout to the Great Lakes must be attributed to early fish culturists who were fascinated by exciting stories about the spectacular California trout. Seth Green, a pioneer New York fish culturist, first brought rainbow trout eggs to eastern North America. These he hatched in 1874, subsequently releasing the young fish into Lake Ontario tributaries with notable success. Other United States fish culturists were soon following Green's example, and by 1882 at least one tributary in each of the Great Lakes had been stocked with rainbow trout."* (MacCrimmon 1977, p. 99)

Fig. 30. Rainbow trout (*Oncorhynchus mykiss*) introduced to the Laurentian Great Lakes drainage basin. *Top photo*: Stream-resident specimen angled in Shelter Valley Creek (Lake Ontario basin) during April 1993. *Bottom photo*: Steelhead angled in the Big Head (Lake Huron basin) during October 1996. Photo credits: Chris Weland.

Rainbow trout and/or steelhead were first released in 1876 to Michigan tributaries of Lake Huron (Smedley 1938; MacCrimmon 1971, 1977; Borgeson 1981; Keller et al. 1989; Kocik and Jones 1999). Over the next decade, stocking expanded to include American waters discharging into each of the remaining Great Lakes (Trautman 1981; Smith 1985). According to some authors (Needham and Behnke 1962; Krueger et al. 1994) rainbow trout were first stocked into Lake Superior in 1883, when fish from the McCloud River were released in the eastern end of the lake. Scott and Crossman (1973) suggested that the stock originally used in introductions was steelhead; however, an examination of the dates cited by these authors suggests that they were unaware of the earliest rainbow trout stocking programs. The steelhead form is known to have been released in 1895 to American tributaries of the remaining upper Great Lakes (Michigan and Huron) by the U.S. Fish Commission (Crossman 1968; MacCrimmon 1977).

The earliest (ca. 1876–1895) rainbow trout eggs for culture and release to eastern North America were obtained from the 'McCloud River' in California (MacKay 1969; MacCrimmon 1977) — very likely the same tributary as the 'McLeod River' cited above as a headwater of the Sacramento River (California) and site of the egg-taking station that provided the first chinook salmon offspring for introduction to the Great Lakes. The rainbow trout from this source became known as the 'Californian trout' or 'shasta trout.' By the mid-1890s, unspecified "*difficulties in maintaining suitable stocks of McCloud River trout developed*" (MacKay 1969), and the American fish culturists turned to other sources of rainbow trout for introduction to the Great Lakes. These new sources included the Klamath River (California) population which was thought to be 'non-migratory' (MacCrimmon 1977), and other rainbow trout populations from Nevada and Colorado (MacKay 1969). It was also during this early explosion of rainbow trout procurements that the steelhead form was known to be taken from Redwood Creek (California) and reared in Great Lakes hatcheries. Thus, from the outset, the rainbow trout introduced to the Great Lakes may have been a complex mixture of strains from a wide variety of native populations.

The early American introductions of rainbow trout to the Great Lakes basin met with a general, yet limited degree of success:

> "*Early optimism that the rainbow trout would adapt to the Great Lakes environment proved to be well founded although there was no spectacular abundance until about the turn of the century.*" (MacCrimmon 1977, p. 100)

Rainbow trout were first captured in Lake Superior by commercial fishermen in 1895 and 1896 (Whitaker et al. 1897). The first capture of rainbow trout in Lake Erie came from deployment of commercial nets in Pennsylvania waters in 1895 (MacCrimmon 1977). In 1896, rainbow trout were first taken in Lake Huron by a commercial pound net operation off Michigan's Upper Peninsula (Radforth 1944). In Lakes Ontario and Erie, populations had become established in American tributaries and shoal waters during the early decades of the 1900s (MacCrimmon 1977). By 1929, Canadian commercial fishermen on Lake Erie were catching rainbow trout; however, these were considered to be the result of intentional releases from American facilities or accidental releases from the Normandale hatchery in Ontario (MacCrimmon 1977).

The major exception to this trend of limited success was the American stocking of steelhead in Lake Superior, which led to "*immediate and spectacular results*" (MacCrimmon 1977). By 1904, the U.S. Bureau of Fisheries stated that spring-spawning steelhead had been reported in "*nearly all the tributary streams along the north shore of the lake*" (i.e., Canadian waters of Lake Superior). By 1905, Lake Superior steelhead were beginning to figure prominently in both the spawning runs and the commercial nets, especially around Thunder Bay and Sault Ste. Marie (Bidgood and Berst 1967; MacKay 1969; MacCrimmon 1977). Rainbow trout occasionally strayed from American to Canadian waters of Lake Huron, but these early movements were apparently infrequent and did not involve great numbers (MacCrimmon 1977). By 1920, self-sustaining populations of rainbow trout were established in Lake Superior tributaries along both the south and north shores (MacCrimmon and Gots 1972).

From an early date, many Great Lakes anglers were extremely excited by the possibility of fishing for rainbow trout, particularly in the tributaries:

> "*The rainbow trout is a popular fish because of its fighting ability, dash and beauty. There is none finer. Its gamey qualities will satisfy the most discriminating. When hooked, it leaps out of the water and rushes and twists with dogged determination and amazing persistence.*" (MacKay 1969, p. 99)

> "*By 1897, the excitement of anglers had reached fever pitch as beautiful fish were harvested from streams and lakes. The western end of Lake Superior was said to be alive with rainbow trout.*" (MacCrimmon 1977, p. 101)

> "*... for the sportsman, the rainbow trout was a gift beyond their wildest expectations. By the turn of the century, trophy fish up to six kilograms were being taken at both ends of Lake Superior.*" (MacCrimmon 1977, p. 101)

However, as MacCrimmon (1977) continues, not everyone was so excited by this introduction to the Great Lakes fish community:

> "*The acclaim accorded the coming of the rainbow trout was not unanimous among sportsmen and naturalists. Many considered this exotic newcomer to be a threat to native fishes, most notably the brook trout whose river habitats were deluged annually by spawning runs of parent rainbows which had grown remarkably while in the open lake.*" (MacCrimmon 1977, p. 101)

It should be noted that commercial fishermen also had 'mixed feelings' about rainbow trout in the Great Lakes.

> "*In some locations, rainbows became a great nuisance to onshore commercial fishermen especially during the fall and spring months, and on occasion these fishermen were forced by the pressures exerted by local anglers to remove their nets from traditional [commercial] fishing grounds.*" (MacCrimmon 1977, p. 102)

Thus, as was the case with both brown trout (Section 2.1.2) and chinook salmon (Section 2.2.1), there was some early opposition to the introduction of a non-native species that could interfere with Great Lakes recreational and commercial fisheries.

To this point, I have described only the actions of state and federal fisheries managers in the United States. The history of rainbow trout introductions by Canadians is less well documented, and at times perplexing. According to Kocik and Jones (1999) Canadian fisheries managers began their introduction of this species in 1881 by releasing steelhead into Lake St. Clair using brood stock from Michigan. The first reference to the release of rainbow trout into Canadian waters of the Great Lakes basin is a letter addressed to the Ontario Department of Game and Fisheries (dated 7 January 1936), by a Mr. T.R. Huxtable of Hornings Mills, Ontario (reprinted by MacKay 1969):

> *"In 1883, the Provincial Government imported rainbow trout from the McCloud River, California, and planted them near Sault Ste. Marie, Ontario. A few years later, an ardent fisherman of that district bought a farm in Hockley Valley, near the source of the Nottawasaga River, twelve miles northeast of Orangeville. On the farm was a real nice tributary of the Nottawa River on which he built a small pond. He then brought down from the Sault some small fry and planted them in his pond, which he screened. A few years later he died. His sons didn't take any interest in fishing or fish, so neglected the dam and it washed out in the spring freshets of 1900, letting the old man's stock of rainbows into the Nottawa River. They evidently worked their way downstream until they found the Pine River. This being a swift, freshwater stream, they followed it up and their first appearance at Terra Nova, 5½ miles east of our dam, was in the year 1903, and the knowledge I had of their being this far upstream was in the fall of 1911."* (MacKay 1969, p. 95)

If the provincial government did take part in early releases of this species, it apparently ceased such activities soon thereafter. As suggested in the letter above, it was private action (intentional or accidental) that was responsible for most of the early rainbow trout stocking in the Canadian waters of the Great Lakes drainage basin. This suggestion is supported by recorded shipments of rainbow trout eggs from the U.S. Bureau of Fisheries to private citizens in Ontario for the purpose of release to the wild — for example, the supply of 20,000 embryos to a private applicant from the Owen Sound (Ontario) region, likely intended for the Sydenham River (MacKay 1969). In 1910, 'enthusiastic' anglers at both ends of the Lake Superior north shore combined resources to purchase rainbow trout for stocking, despite the fact that rainbow trout had already established reproducing populations in many of these tributaries (MacCrimmon 1977). Apparently, stocked steelhead reproduced in coldwater tributaries, and self-sustaining populations developed in all five of the Great Lakes by the early 1900s (MacCrimmon and Gots 1972; Biette et al. 1981; Kocik and Jones 1999).

After 30 years of intensive rainbow trout stocking by U.S. fisheries interests (government and private) and by private citizens in Ontario, the Canadian federal and provincial governments began to release rainbow trout in Canadian waters. Apparently, this decision was lobbied by the angling community, and was made reluctantly by government fisheries managers:

> *"... the arrival of rainbow trout to the Great Lakes basin was a low-key affair and was not accorded the fanfare which was to be bestowed on the species in later years. However, those anglers who caught the rainbow trout were enthusiastic over the fighting and eating quality of this attractive exotic. Perhaps the recoveries were too few and to [sic] localized to attract much attention. Nevertheless, from a small minority of anglers came pressure for government agencies on both sides of the Great Lakes to move more actively into the culture and release of rainbow trout secured from various west coast stocks. ... By 1912, the Canadian government had been talked into a limited rainbow trout stocking program."* (MacCrimmon 1977, p. 101)

The Province of Ontario began rearing rainbow trout from the original McCloud strain at the Mount Pleasant Hatchery near Brantford in 1914, transferring hatchery operations to the Normandale facility four years later (MacCrimmon 1977). By 1918, the Ontario Department of Game and Fisheries had finally put aside its reservations on rainbow trout introduction to the Great Lakes and entered into an intensive stocking program (MacKay 1969). At this time, the provincial fisheries management policy stated its goal to be the development of wild-reproducing, self-sustaining populations of rainbow trout in all Canadian waters of the Great Lakes. Steps were taken to establish sanctuaries to protect those tributaries where the rainbow trout were known to spawn (MacKay 1969). In 1922, the Ontario government began its intensive stocking program in Lake Huron and Georgian Bay (MacCrimmon 1977). After 1929, the Ontario government undertook regular plantings of rainbow trout in Lake Erie tributaries, primarily streams in Norfolk and Oxford Counties (MacCrimmon 1977).

The 1904 capture of an adult rainbow trout, south of Manitoulin Island (Lake Huron), has been suggested as the first documented occurrence of wild rainbow trout in Canadian waters of the Great Lakes proper (Radforth 1944). Shortly thereafter, rainbow trout were making seasonal migrations between the Nottawasaga River and Georgian Bay; these fish likely resulted from the private release of rainbow trout in the Nottawa River, a headwater of the Nottawasaga (see above). The American steelhead planting in Lake Superior had also resulted in the migration of these fish to Canadian open waters and tributaries by 1904 (Radforth 1944).

In general, rainbow trout were uncommon in Ontario tributaries of Lake Huron until 1915 (MacCrimmon 1977). By 1920, large rainbow trout were being harvested by commercial fishermen around Southampton; these fish were attributed to a strong population in the Saugeen River as a result of the earliest stocking efforts of Canadian hatcheries. By 1922, Canadian stocking efforts had apparently established abundant populations in most of its tributaries to the upper Great Lakes (MacCrimmon 1977). Despite Ontario's stocking efforts in Bronte Creek and the Humber River since 1922, it was not until releases from the Codrington hatchery into Wilmot Creek began in the early 1940's that abundant rainbow trout populations were established in Canadian Lake Ontario tributaries. The first confirmed spawning of rainbow trout in a tributary to Lake Ontario was reported in Dufferin Creek in 1947 (MacCrimmon 1977). Subsequently, intensive rainbow trout stocking programs resulted in abundant populations in most Lake Ontario tributaries which had originally supported Atlantic salmon populations (MacCrimmon 1977).

In the 1930s, fish culturists in Minnesota began a new initiative in rainbow trout stocking in the Great Lakes drainage basin. They had successfully manipulated the life-history of the typical spring-spawning rainbow trout to become a fish that would spawn between November and January (MacKay 1969; MacCrimmon 1977). In 1934, the Ontario Department of Game and Fisheries imported a supply of these 'Missouri rainbows' from the Minnesota hatcheries and began releasing this new form into Canadian waters.

In contrast to the results achieved with other Pacific salmonines, proponents of early rainbow trout introductions were generally pleased with their efforts. Rainbow trout populations expanded rapidly in Great Lakes tributaries, despite drastic declines in the 1940s and 1950s attributed to sea lamprey parasitism (Berst and Wainio 1967). By 1960, rainbow trout had become firmly established in all parts of the Great Lakes drainage basin. This was due, in large part, to the fact that rainbow trout exhibited a greater ability to reproduce in Great Lakes tributaries than the other Pacific salmonines (MacCrimmon 1977). Wild rainbow trout enhanced the stocking programs of both American and Canadian fisheries agencies by establishing wild-reproducing populations, and by dispersing. By 1960, the rainbow trout was considered a "*valuable tool*" for fisheries managers in the Great Lakes:

> "*The rainbow trout has been introduced to Ontario waters with considerable success and is rated as one of the most important sport fishes inhabiting certain inland lakes, the Great Lakes and their numerous large tributaries. In these areas, the rainbow trout is a potential money-maker. It should flourish in the years ahead if angling is not permitted to deteriorate through depredation by the predator lamprey, by poaching or by illegal netting.*" (MacKay 1969, p. 100)

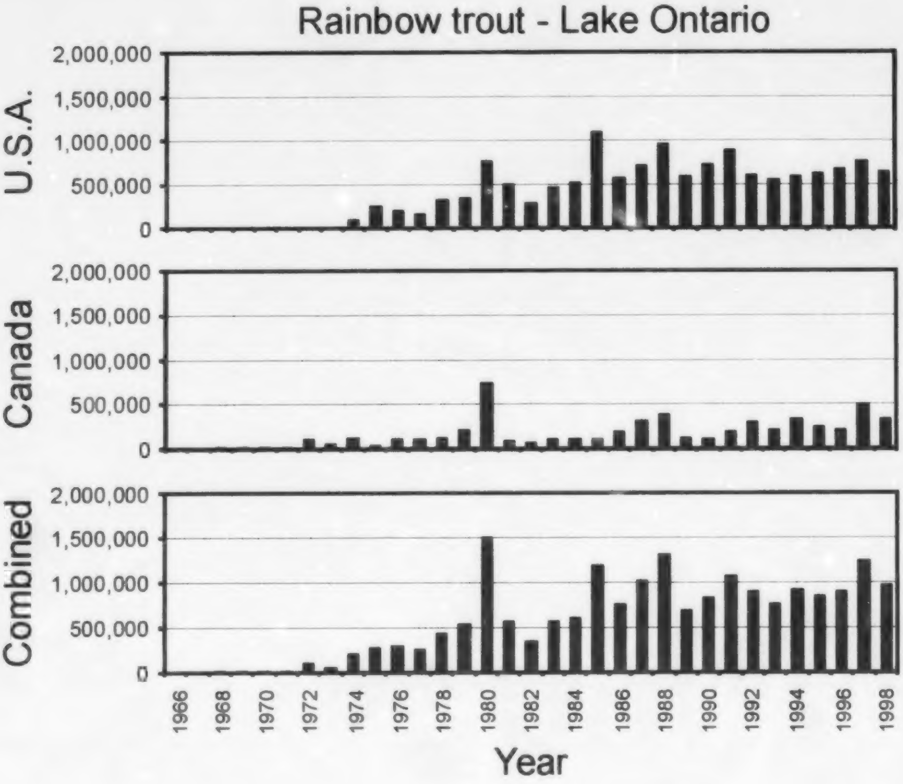
Thus, for the early period of salmonine introductions to the Great Lakes, rainbow trout was considered a success.

Rainbow trout continued to be the focus of stocking programs throughout the recent era. The primary purpose of these stocking programs was to support recreational fisheries, rather than to engage in some form of biological control. Tody and Tanner (1966) suggested that it would be possible to increase rainbow trout populations through stocking programs; however, they felt it was doubtful that the steelhead would consume more alewife in the Upper Lakes than coho or chinook salmon. In addition, these authors suggested that rainbow trout was more difficult and more expensive to stock than other Pacific salmonines. By itself, the State of Michigan annually stocked an average of approximately 1 million rainbow trout into the Great Lakes drainage basin from 1960 to 1980 (Emery 1985). The steelhead recreational fishery grew, especially in Lakes Superior, Michigan and Huron. From 1970 to 1983 the estimated recreational harvest of rainbow trout (including steelhead) in Michigan exceeded 300,000 fish per year (Emery 1985).

During the period 1966 to 1998; a total of 174 million rainbow trout have been introduced to the Great Lakes ecosystem (Appendix I). In Lake Ontario and Lake Erie, rainbow trout releases have generally increased, with a predominance of American hatchery stocking (Figs. 31, 32). In Lake Huron, rainbow trout stocking increased to maximum levels of approximately 2 million fish per year during the late 1980s, with a reduction over the 1990s to roughly one half (Fig. 33). Stocking of rainbow trout in Lake Superior has been erratic during the modern era; from lows of a few hundred thousand fish per year, to maxima of more than 3 million fish — all of which have been stocked by American agencies or licensed sportsmen's groups (Fig. 34). When viewed across the Great Lakes, it can be seen that approximately one-third of all 174 million rainbow trout releases have occurred in Lake Michigan — relatively low levels of stocking in most other lakes have been relatively consistent (Fig. 35). Once again, American hatcheries have been responsible for the vast majority of rainbow trout introductions in the modern era, with approximately 87% of the total 174 million fish stocked (Appendix I).

While rainbow trout have been reported to reproduce throughout the Great Lakes basin, many of the populations are considered to be highly dependent on hatchery stocking programs for their continued existence (Emery 1985; Mills et al. 1993; Marcogliese and Casselman 1998). In Lake Huron, the sport salmon fishery is "*increasingly supported by stocked rainbow trout, and the abundance of wild fish has declined (LHMU 1994)*" (Bence and Smith 1999). Even with stocking programs (and

Fig. 31. Number of rainbow trout (*Oncorhynchus mykiss*) stocked by jurisdiction in Lake Ontario for the period 1966–1998.



perhaps because of them), rainbow trout populations are vulnerable to unexplained population fluctuations, and even local extinctions (LHMU 1995; Negus 1999).

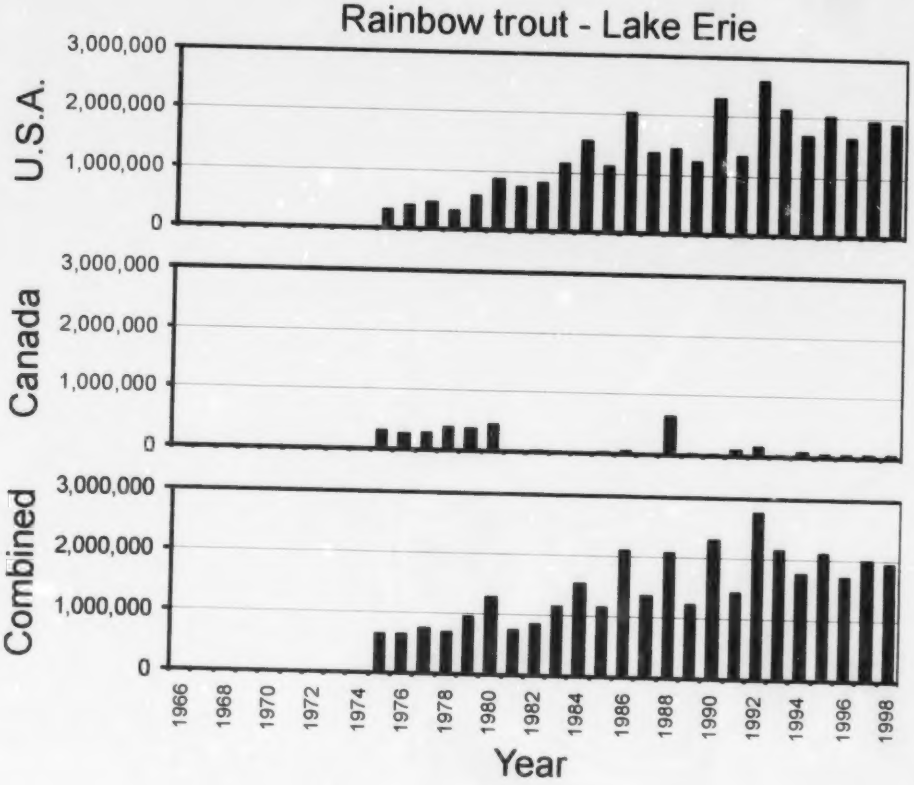
The objections raised against introduction of rainbow trout to the Great Lakes did not disappear by the end of the early history. For example:

> *"Even today the argument over the compatibility of the two species [rainbow and brook] continues among trout fishermen, although there is strong evidence that environmental change was the principal culprit in decimating brook trout populations in the lower reaches of many watersheds now inhabited by the rainbow trout."* (MacCrimmon 1977, p. 101)

Thus, there still appears to be a latent form of objection to this, the most 'successful' and 'universally accepted' of salmonine introductions to the Great Lakes. It was as if the original objections were never addressed.

Recently, angler interest caused fisheries managers to introduce an artificially generated form of rainbow trout which enters Great Lakes tributaries during summer

Fig. 32. Number of rainbow trout (*Oncorhynchus mykiss*) stocked by jurisdiction in Lake Erie for the period 1966–1998.



months when few other introduced salmonines are available to the recreational fishery (Seelbach et al. 1994). In 1975, Indiana began introducing summer-run or 'skamania' steelhead into Lake Michigan (Rand et al. 1993). These skamania were generated through genetic selection of a Washington hatchery strain (Seelbach and Whelan 1988; Rand et al. 1993). Skamania were stocked for the first time in Ontario waters of the Great Lakes in 1989 near Owen Sound, however American releases had previously been captured in the Saugeen River drainage basin (Smith 1991). This strain of rainbow trout was selected for management by the Ontario Ministry of Natural Resources because of its early spawning and its reported 'fighting' capabilities (OMNR 1987).

Fig. 33. Number of rainbow trout (*Oncorhynchus mykiss*) stocked by jurisdiction in Lake Huron for the period 1966–1998.

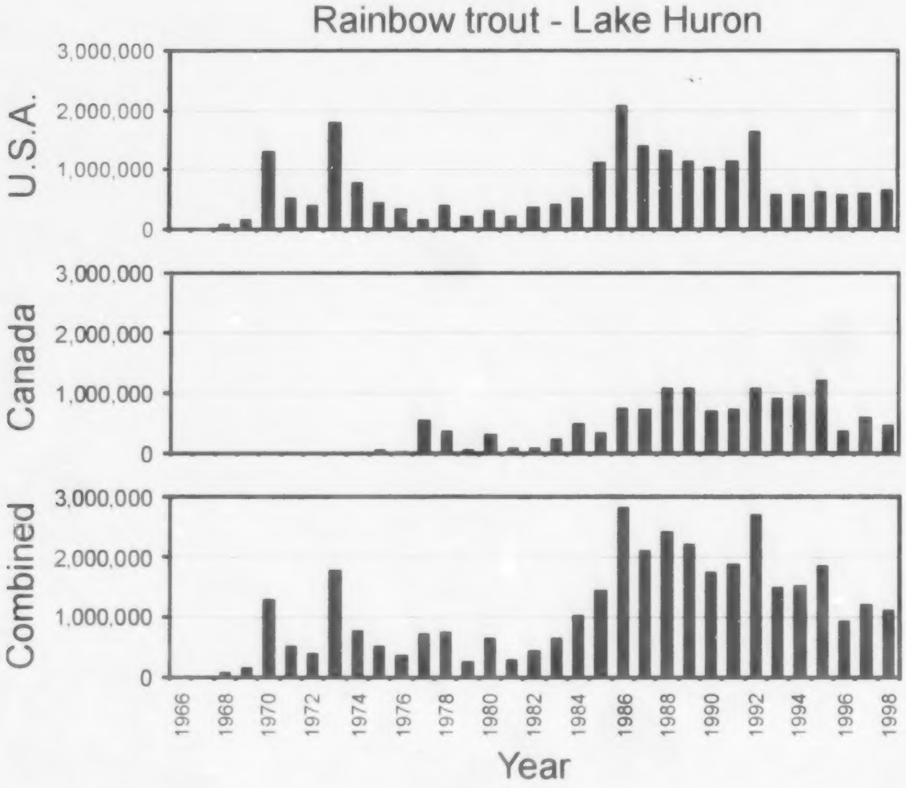


Fig. 34. Number of rainbow trout (*Oncorhynchus mykiss*) stocked by jurisdiction in Lake Superior for the period 1966–1998.

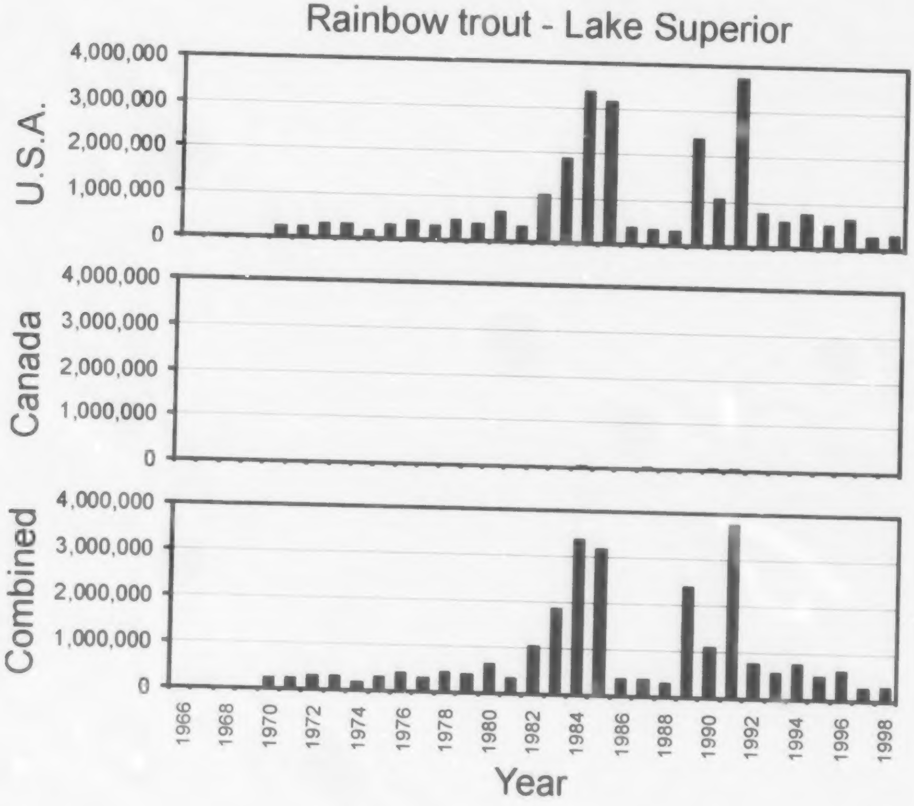
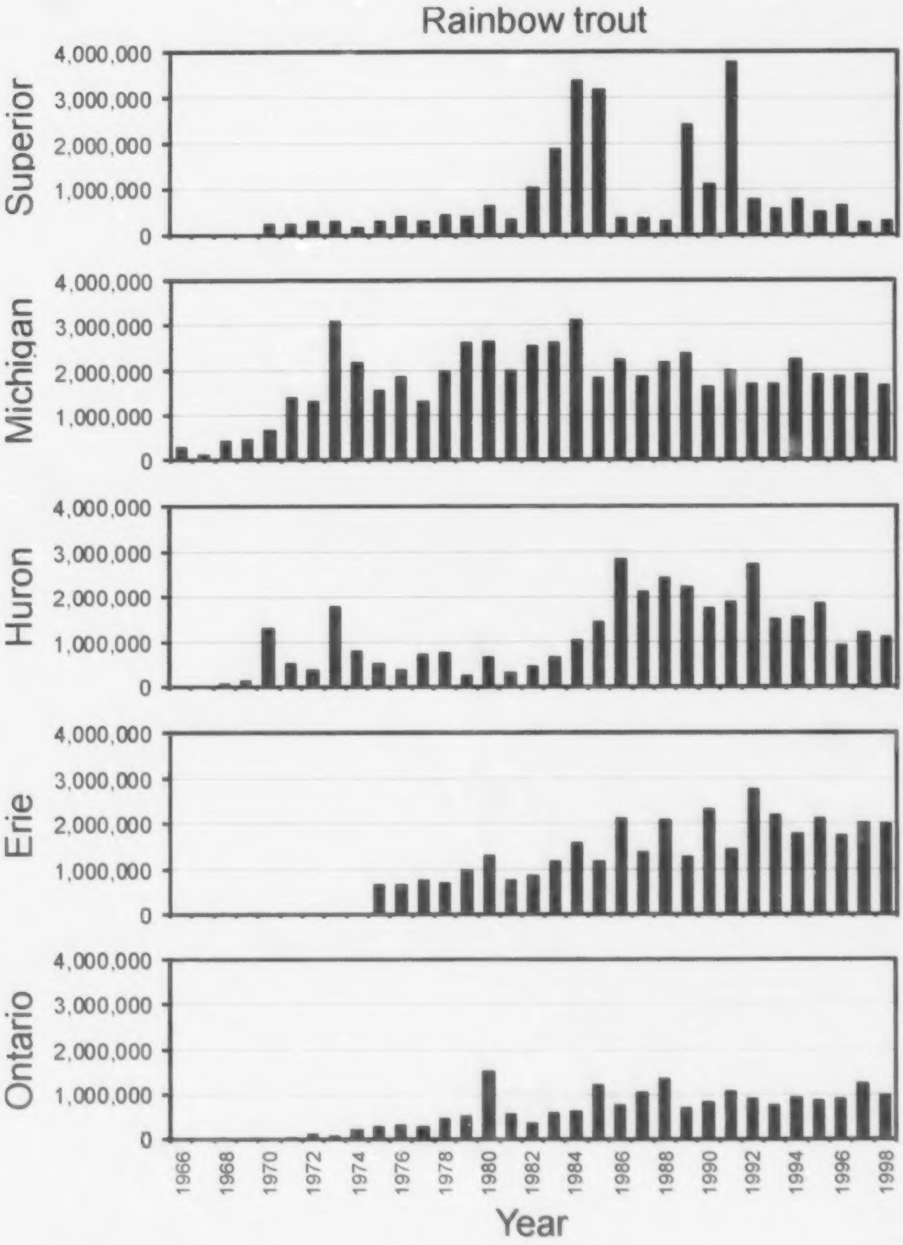


Fig. 35. Number of rainbow trout (*Oncorhynchus mykiss*) stocked in each of the Laurentian Great Lakes for the period 1966–1998.



2.2.4 Kokanee (*Oncorhynchus nerka*)

Kokanee is a permanently freshwater form of sockeye salmon, a species native to the Pacific Ocean and its tributaries from Alaska (and occasionally the Arctic Ocean) southeast to the Klamath River in California, and southwest along the Asian coast to Japan and the Anadyr River on the mainland:

> *"It occurs naturally in many lakes to which anadromous salmon no longer have access, but must have had at one time. The extent of the distribution of true kokanee populations may be clouded by the presence in various freshwater localities of "residual" populations of sockeye that do not reproduce."* (Scott and Crossman 1973, p. 167)

Thus, kokanee have a native distribution geographically similar to the other Pacific salmonines; this particular form of the species is usually associated with landlocked waters.

The first documented introduction of kokanee to the Great Lakes occurred in 1950, when the New York government stocked kokanee juveniles in Lake Ontario tributaries (Parsons 1973; Emery 1985). Apparently, these kokanee were intended to support a recreational fishery, despite the fact that this form of the species preys on plankton rather than on larger prey fishes:

> *"Kokanee have long been a sport fish of interest, at least at certain times of the year, in their natural range. They gained even more prominence when moved to areas where anglers did not have an abundance of other salmonids. They are often looked upon as difficult to catch when the angler learns they are plankton feeders. They are, however, rather readily taken fishing rather shallow with a flashy metal troll (willow leaf troll) of various patterns, with a small baited hook attached."* (Scott and Crossman 1973, p. 170)

While some kokanee were captured in Lake Ontario tributaries in 1950, the program was terminated shortly thereafter — probably due to the inability of these fish to establish self-sustaining populations in the wild.

In 1964, F.P. Maher of the Ontario Department of Lands and Forests authored a report on the feasibility of introducing kokanee to the Great Lakes. Although not clearly stated in Maher's (1964) proposal, the objectives for introducing kokanee to the Great Lakes can be gleaned from the following statement:

> *"Since past experiments with the planting of salmon in the Great Lakes have been disappointing, it might be considered overly optimistic to expect any better results from the planting of yet another species. This report will concern itself with the reasons why it is believed that the introduction of kokanee has a reasonable chance of developing a self-perpetuating population of desirable fish, to supplement stocks of desirable indigenous species which have declined greatly in numbers in recent years."* (Maher 1964, p. 2)

The principal objective for introducing kokanee was the establishment self-sustaining populations primarily to support recreational and perhaps commercial fisheries, and secondarily as a forage species for lake charr (see also Collins 1971).

Although not highlighted in Maher's (1964) proposal, other authors cited alternate objectives for introducing kokanee, in addition to reversing the decline of traditional fisheries. It was thought that kokanee might also replace decimated lake herring

(= cisco) populations (i.e., niche filling objective; Scott and Crossman 1973), and in turn serve as prey for piscivorous species (forage objective; Christie 1968):

> "*Kokanee were introduced into Lake Huron at a time when the ecosystem was in an exceptional state of flux ... As well as being a potentially valuable fishery resource, kokanee may serve a secondary function as a forage fish.*" (John C. Collins, 1971 in MacCrimmon 1977, p. 140)

Tody and Tanner (1966) thought that kokanee could also serve as planktivore competitors to diminish the trophic dominance of the introduced alewife. This objective was interpreted as being a form of biological control, in addition to direct predation objectives for the larger salmonines.

Maher's (1964) proposal for introducing kokanee to the Great Lakes was presented in a somewhat similar manner to the later proposal of Tody and Tanner (1966) for coho salmon (see Section 2.2.2), including:

- a review of life-history characteristics of this species in its native range,
- discussion of the potential adaptability of kokanee salmon to the Great Lakes and
- presentation of plans for introduction, including stocking methods and procedures.

In his report, Maher (1964) explicitly recognized the concern that had developed regarding the continued introduction of non-native salmonines to the Great Lakes ecosystem:

> "*It is natural to expect some anxiety on the part of fishery workers over the introduction of a new species of fish to the Great Lakes region. There are those who feel strongly that indigenous species should be further developed if at all possible, rather than to attempt new fisheries with new species. ... One introduction which was planned, that of the rainbow trout, has been most successful. Since introductions are occurring whether planned or not, it seems sensible to attempt the deliberate introduction of a species which, according to the best information available, would be an asset to the Great Lakes fishery.*" (Maher 1964, p. 21)

Maher's (1964) tactic was to justify additional, intentional introductions on the basis that unplanned introductions were continuing; his ultimate criterion for determining the appropriateness of an introduction was the benefit to the fishery, rather than the ecosystem that supported the fishery.

Other fisheries scientists expressed concerns about the lack of appropriate ecological evaluation of the proposed kokanee introduction to the Great Lakes:

> "*Both [kokanee and coho salmon] were earmarked for subsequent releases into Great Lakes waters amid dissenting views on the desirability of introducing such potentially prolific exotics without any knowledge of their likely impact on native fauna.*" (MacCrimmon 1977, p. 142)

These concerns were amplified by the fact that kokanee were known to have a high rate of population growth:

> "*The fact that [kokanee] can develop extremely large populations (14 tons were seined from Christina Lake, B.C., in a single night in 1898–1899) makes them*

> *both useful and potentially dangerous in exotic situations.*" (Scott and Crossman 1973, p. 170)

At the conclusion of his proposal, Maher (1964) presented the following arguments in defense of the ecological appropriateness of kokanee introductions to the Great Lakes:

> "*... it is difficult to see what harm could result by introducing kokanee to the Great Lakes. The reasons for adopting this view can be summarized briefly as follows:*
>
> 1. *Kokanee are a pelagic fish for most of their lives, and subsist largely on zooplankton. They could be expected to occupy open water areas of the lakes which are now largely unproductive of desirable species.*
> 2. *Because of their pelagic, zooplankton feeding habit, kokanee are able to thrive in bodies of water with limited bottom fauna production.*
> 3. *Unlike other species of salmon stocked previously, the kokanee has become adapted to fresh water life.*
> 4. *Kokanee are able to spawn in a wider variety of habitats than other salmon. It is difficult to assess spawning areas in the Great Lakes which might be suitable for them, but it would be surprising if some suitable spawning grounds were not discovered by these fish.*
> 5. *Should they by chance find such suitable spawning grounds that they become over-abundant, the worst that would likely happen is that a large population of small desirable fish would be available. Even so, they would be occupying a part of the lake which at present is not used to any extent by desirable species.*
> 6. *If it is found that suitable spawning grounds are inadequate, or totally lacking, artificial stocking could be considered. Because of the strong homing tendency of kokanee, it is possible that local populations could be maintained by fry liberations. Returns from some California fry plantings have been so high it has been estimated that each fish creeled cost an average of two cents. The cost per fish could be several times this amount and still make artificial propagation economically feasible.*
> 7. *It has been amply demonstrated that kokanee are suitable as forage for trout in large lakes. Experiences in small lakes (less than three or four square miles) have shown that kokanee can out-compete trout for food and apparently cause a reduction in the trout population. This relationship has never been demonstrated in the larger lakes, and in fact several authorities attribute good trout fishing in larger western lakes to the presence of kokanee.*
> 8. *Kokanee have a high value as both a game and table fish.*
> 9. *Because they are salmon, they can be expected to have a popular appeal which will make them readily marketable should they become abundant enough to warrant establishment of a commercial fishery.*
> 10. *Kokanee now attain an attractive size, 12 to 18 inches in length, in productive lakes elsewhere, even though coming from stock which mature at a much smaller size in their native waters. There is every rea-*

> *son to suppose that kokanee planted in the Great Lakes would grow to at least 14 inches in length. They have shown amazing growth when feeding on* Mysis *in Kootenay Lake, and these organisms are present in the Great Lakes. The Great Lakes are more productive than the larger western lakes in which kokanee now do well, and it is most unlikely that a stunted population of kokanee would develop.*
>
> *11.* *Larvae of the broad fish tapeworm* Diphyllobothrium latum *have been found in kokanee from Kootenay Lake. Since kokanee would be brought to Ontario from the west as eyed eggs, the parasite could not be brought in to the area. In any event, the parasite is now present in the Great Lakes in other fish. It is not considered likely that kokanee would become heavily enough infested to create a problem. Even in Kootenay Lake the incidence of parasitism by* Diphyllobothrium *is not great, and does not detract from the value of the fish for sport or table use."* (Maher 1964, p. 22)

If readers are somewhat confused by this list of statements, there is a very good reason. This is actually a list of reasons for expecting that kokanee would succeed in the Great Lakes. None of these statements can be construed as reasons for thinking that the introduction of kokanee to the Great Lakes would be harmless, at least in an ecological sense. At best, statement #1 suggests (without theoretical or empirical support) that kokanee might exist in spaces of the lake where 'desirable' species (presumably meaning economically desirable species) did not frequent. At worst, statements #5, #7 and #10 suggest that kokanee could actually become 'overabundant,' intense competitors with 'trout' (presumably including lake charr). Maher (1964) did not provide any reasoning or evidence that kokanee would behave in a benign manner in the Great Lakes.

In 1964, the Province of Ontario requested and received a shipment of 1.5 million embryos from Kootenay Lake stream-spawners in British Columbia (Scott and Crossman 1973; MacCrimmon 1977). Over the next year, the Province of Ontario began releasing these kokanee in tributaries and open waters of Lakes Huron and Ontario (Parsons 1973; MacCrimmon 1977; Collins 1971):

- Lake Ontario: Shelter Valley Creek and Wilmot Creek (approx. 350,000 eggs)
- Lake Huron: tributaries on the Bruce Peninsula, Manitoulin Island, and south eastern Georgian Bay (approx. 350,000 eggs)
- Lake Huron and Lake Ontario open water shoals (approx. 800,00 embryos)

Over the next few years, more than 4 million additional kokanee embryos were obtained from a stream-spawning population in Idaho, and lake-spawning populations in Colorado, Oregon, Washington and Montana (Crossman 1968; Scott and Crossman 1973; MacCrimmon 1977) and released (Collins 1971). Approximately 17 million kokanee were released into tributaries and open waters of the two lakes before the stocking program was terminated in 1972 (Emery 1985).

In Lake Huron, commercial fishermen began catching numerous kokanee off the eastern end of Manitoulin Island, in tributaries around the Bruce Peninsula and southwestern Georgian Bay where plantings had been concentrated (Collins 1971; MacCrimmon 1977). In the autumn of 1967, large spawning runs were observed in at least 10 tributaries of Lake Huron. The largest runs appeared in Manitou River and

Blue Jay Creek on Manitoulin Island, and in Oxenden Creek in southwestern Georgian Bay (Collins 1971; MacCrimmon 1977).

It appeared that the spawning kokanee returned, in some degree, to the tributaries in which they had been released as well as running up rivers which had not been stocked (Crossman 1968). Moreover, there was evidence of open-lake shoal spawning by kokanee around Manitoulin Island (Collins 1971; MacCrimmon 1977). Detailed observations on the fate of the first kokanee releases were made in Blue Jay Creek on Manitoulin Island (Porter 1972) and in the Sydenham River in southwestern Georgian Bay (MacCrimmon 1977). Successful stream spawning in 1967 was indicated by retrieval of live eggs and alevins from redds, and capture of downstream offspring (Collins 1971). Apparently, there was a high survival rate after hatching, followed by downstream migration to the open lake. The large runs of kokanee in certain tributaries of Lake Huron excited local anglers (MacCrimmon 1977).

The success of kokanee in Lake Huron was relatively short-lived. By the early 1970s, the spawning runs had pretty much ceased, due to a combination of reduced stocking programs and the inability of the introduced kokanee to establish self-sustaining populations through wild reproduction (MacKay 1969; MacCrimmon 1977; Emery 1985).

After 'generously' stocking kokanee embryos into Lake Ontario tributaries for several years (3.3 million fish released 1968–1972; GLFC 2000), very few adults were taken by either commercial or recreational fishermen (MacKay 1969; MacCrimmon 1977). No confirmed spawning runs developed in the basin, and there was no evidence of successful reproduction.

All kokanee stocking programs were terminated by the Province of Ontario in 1972 (Mills et al. 1993):

> *"Spawning populations in most rivers seemed to [decline dramatically after initially high numbers] and, although sporadic runs still occur in several watersheds, so discouraging was the general situation that interest in the kokanee waned almost as rapidly as it had been aroused."* (MacCrimmon 1977, p. 144)

Apparently, there was also minor interest expressed in the kokanee by American fisheries managers (Smith 1968; MacKay 1969; Scott and Crossman 1973) — notably, the States of New York (Lake Ontario) and Michigan (Lakes Superior, Michigan and Huron). There does not appear to be any published documentation of these introduction efforts.

After the stocking programs ceased, the wild kokanee populations in Lake Huron declined, and faded to near extinction (Emery 1985; Mills et al. 1993). Small numbers (i.e., <10 individuals) of kokanee have been reported in Blue Jay Creek (Lake Huron, Manitoulin Island) as recently as 1993 (Kocik and Jones 1999).

2.2.5 Chum salmon (*Oncorhynchus keta*)

Chum salmon are native to the Pacific and Arctic Oceans, and their tributaries, southeast to the Sacramento River and southwest to Korea (Scott and Crossman 1973).

From 1908 to the early 1940s, hatcheries in Michigan, Pennsylvania and Wisconsin provided juvenile chum salmon for release into waters of Lake Superior and Lake Huron (MacCrimmon 1977). The purpose of these early introductions is rather unclear, especially considering the relatively low esteem with which anglers hold the species (Scott and Crossman 1973). The modest intensity of chum salmon introductions to the Great Lakes did not result in self-sustaining populations; stocking programs were terminated by 1945 (MacCrimmon 1977).

2.2.6 Cutthroat trout (*Oncorhynchus clarkii*)

Cutthroat trout is native to the Pacific Ocean and its tributaries from southeastern Alaska to the Eel River in northern California, and also in a disjunct range east of the Rocky Mountains in Alberta and a few of the northern states (Scott and Crossman 1973).

As with the rainbow trout (Section 2.2.3), the cutthroat trout was classified in 1836 as a member of the Atlantic salmonine genus *Salmo*; it too has been reclassified into the complex of Pacific salmons in the genus *Oncorhynchus* (Smith and Stearley 1989). This species exhibits a remarkable diversity of body form, with an anadromous (marine–freshwater) form called 'coastal cutthroat' and a nonanadromous or 'potamodromous' (freshwater, see Kocik and Jones 1999) form called 'Yellowstone cutthroat' (Scott and Crossman 1973).

In the early 1890s, the State of Michigan received Yellowstone cutthroat trout from an American federal fish hatchery in Colorado (Worth 1895), and these fish were introduced into the Pere Marquette River of Lake Michigan (Emery 1985). From 1895 to 1940, Michigan released 105,000 cutthroat trout in its waters; however, none of these fish were captured (Holcomb 1964). The States of Minnesota and Wisconsin acquired this species from the same hatchery in 1892 (McDonald 1895); however, it is unclear whether these fish were released to the wild (Emery 1985).

In the early 1950s the State of Michigan sporadically released Yellowstone cutthroat trout to its Great Lakes tributaries (at least Lakes Michigan and Huron), with the resulting establishment of temporary populations (Hubbs and Lagler 1958). However, by 1958 this species was rare or extinct in the Great Lakes basin (Hubbs and Lagler 1958).

According to Scott and Crossman (1973), cutthroat trout may also have been introduced to Georgian Bay (Lake Huron) by Ontario fisheries managers; however, neither the year(s) of release nor the results were documented.

2.2.7 Masu salmon (*Oncorhynchus masou*)

The masu salmon is native to Japan, where it is land-locked in certain lakes and small streams (Christie 1968). In 1929, a small number of masu salmon were imported from Japan by the State of Michigan, and released into a tributary of Lake Michigan (Westerman 1930). In his subsection on masu salmon in the Great Lakes, Parsons (1973) described this attempted introduction as follows:

> "*About 200 fingerlings (18 months old) were planted in the North Branch of the Boyne River in Charlevoix County, Michigan, in 1929, No survivors were reported* (F.A. Westerman, personal communication; letter to Carl. L. Hubbs, March 31, 1930)." (p. 42)

Apparently, there were no survivors of this introduction.

2.2.8 Pink salmon (*Oncorhynchus gorbuscha*)

The pink salmon (Fig. 36) is native to the Pacific Ocean and its tributaries from the Arctic Ocean near the Bering Strait, southeast to the Sacramento River in California, and southwest to Peter the Great Bay in Asia.

In September 1959, two Minnesota anglers fishing near the mouth of Cross Creek — a Lake Superior tributary — caught two pink salmon that were nearing sexual maturity (Schumacher and Eddy 1960; Schumacher and Hale 1962; MacCrimmon 1977). Shortly thereafter, other pink salmon were reported in American waters of Lake Superior, near the mouths of the Manitou River and Sucker Creek (MacKay 1969). The first reports of pink salmon in Canadian waters were based on a single adult specimen captured by a commercial fisherman in Black Bay (Scott and Crossman 1973, year not reported), and from the mouth of the Pigeon River (MacKay 1969), both in the Lake Superior drainage basin.

American and Canadian fisheries managers were at a loss to explain how these pink salmon arrived in Lake Superior — there were no records of any previous attempt to introduce this species anywhere in the Great Lakes!

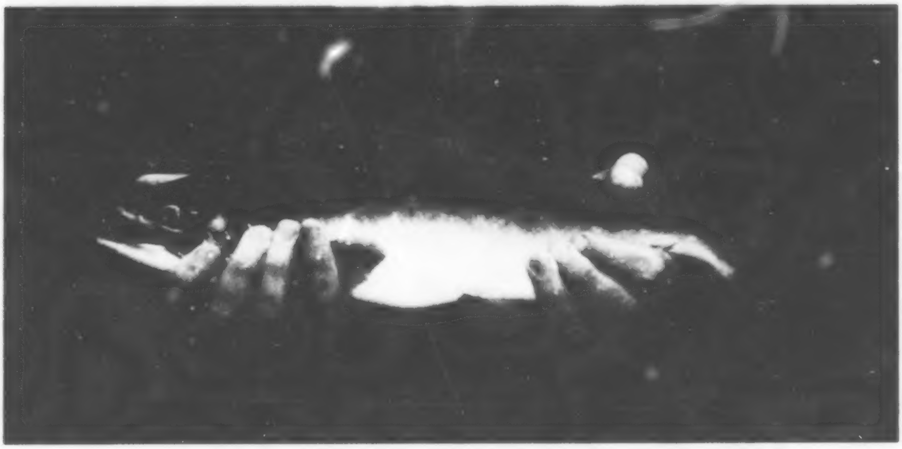
After a frantic investigation, it became clear that pink salmon had in fact been introduced to the western Lake Superior drainage basin during unauthorized actions at the Port Arthur Fish Hatchery on the Current River in Ontario. This hatchery was serving as a rearing facility for pink salmon destined for Goose Creek in the Hudson Bay drainage basin (Ricker and Loftus 1968). Pink salmon eggs had been collected in 1955 from the Skeena River in British Columbia, and then transported to the hatchery for incubation before being air-lifted for release (Ricker and Loftus 1968; MacKay 1969; source reported as the Lakelse River by Kocik and Jones 1999). The hatchery had released pink salmon on several occasions:

> "*At the hatchery it was admitted that not only had a few hundred young pink salmon escaped into the Lake during the loading of an Otter aircraft in 1956, but that several thousands of young fish had been discarded into a sewer discharging into the Current River through which there was ready access to Lake Superior.*" (MacCrimmon 1977, p. 148)

> "*Although several different releases occurred, the disposal by hatchery managers of excess stock, about 21,000 fingerlings, into the Current River after the Hudson Bay stocking program had been completed, is probably the source of the Great Lakes pink salmon population. It was believed from knowledge of the reproductive biology and ecology of the species that these fingerlings would not establish reproducing populations in Lake Superior. In addition to the excess stock, other introductions occurred at the hatchery either as escapees during the transfer of fish to planes for transport to James Bay or as accidental releases into Lake Superior with the stocking of lake trout fingerlings.*" (Mills et al. 1993, p. 10)

Thus, pink salmon were released through a combination of accidents in technical operations, and by the intentional discharge of excess stock into the Current River (see also Nunan 1967; Collins 1975).

Fig. 36. Pink salmon (*Oncorhynchus gorbuscha*) introduced to the Laurentian Great Lakes drainage basin. Stream-run male, angled from the Pancake River (Lake Superior basin) in September 1998. Photo credit: Chris Weland.



The rationale of the Port Arthur Fish Hatchery staff for discharging their excess pink salmon into the Current River was associated with the prevailing attitude that this species would not successfully establish self-sustaining populations in the Great Lakes drainage basin:

> *"Not long before [the first capture of pink salmon in Lake Superior] had come a scientific pronouncement that the pink salmon could not reproduce successfully without spending some time in a marine environment."* (MacCrimmon 1977, p. 147)
>
> *"[The first reports of adult pink salmon in Lake Superior] created widespread interest because there are few undoubted instances of the completion of the life cycle of the pink salmon in freshwater."* (MacKay 1969, p. 266)

This paradoxical belief was not well documented; however, it was probably based on the previous experience of Great Lakes fisheries managers with other Pacific salmonines (except of course, the rainbow trout). At any rate, this belief persisted in the response of fisheries managers after they had learned of the pink salmon releases from the Port Arthur facility:

> *"In 1956 some surplus pink salmon fry were released into Lake Superior by the Ontario Department of Lands and Forests. Fragmentary reports indicate that some survived and spawned, but since little factual information is available it is difficult to assess the success of the introduction. Because of its life history in its native waters, and its failure to establish a fresh water form there, it seems probable that pink salmon may not become established in Lake Superior."* (Maher 1964, p. 1)

The public alarm regarding pink salmon introductions to Lake Superior declined along with the capture rates of these animals by recreational and commercial fishermen. However, this trend changed in 1961, when mature pink salmon re-appeared after three generations, consistent with what was then considered an invariant 2-year life cycle (Scott and Crossman 1973; MacCrimmon 1977; Nicolette and Spangler 1986). These mature pink salmon were observed in tributaries along the shores of Lake Superior from Minnesota to the Nipigon River — this time with evidence of reproduction (Schumacher and Hale 1962; MacCrimmon 1977). The abundance of pink salmon at river mouths had apparently declined by the period from 1963 to 1967 (Scott and Crossman 1973), leading to the re-speculation by fisheries managers that the pink salmon would ultimately fail to establish self-sustaining populations in the Great Lakes. However, progressively stronger spawning runs of pink salmon during odd-numbered years were observed in Minnesota and Ontario tributaries to Lake Superior in 1969, 1971 and 1973 (Lawrie and Rahrer 1972, 1973; MacCrimmon 1977).

Within Lake Superior, the pink salmon exhibited a significant ecological innovation by establishing new spawning runs. In 1976, Kwain and Chappel (1978) found spawning, and spent, 2-year-old pink salmon in the Steel River, Ontario; a 3-year-old pink salmon was caught in a Michigan tributary of Lake Superior (Wagner 1978). Evidently, Great Lakes pink salmon had switched from their the normal 2-year cycle (odd-years) of reproduction to both 3-year-old spawning runs (Collins 1975; Kwain and Chappel 1978; Wagner and Stauffer 1980; Nicolette 1983), and to precocious 1-year-old spawning runs (Kwain and Kerr 1984). This was a remarkable shift in reproductive ability that had the effect of increasing total reproductive contribution over time.

Since 1958, small but increasing numbers of pink salmon were taken by commercial and recreational fishermen (Scott and Crossman 1973). Moreover, the pink salmon in Lake Superior soon spread to Lake Huron, where spawning in tributaries was first observed in 1969 (Collins 1975). The pink salmon migrated and established populations in each of the remaining Great Lakes: Michigan in 1973, Lakes Erie and Ontario by 1979 (Kwain and Lawrie 1981; Kwain 1982; Wagner and Stauffer 1982; Ryder and Edwards 1985). This represented a colonization of all 5 Great Lakes without supplemental stocking, in a mere 10 generations (Emery 1985; Kwain 1987).

By 1973, there were even documented accounts of pink salmon in the St. Lawrence River near Montreal Island (Scott and Crossman 1973). Peak spawner densities were observed in U.S. tributaries of Lake Superior in 1979 when many streams experienced runs of 10,000 fish or more (Borgeson 1981; Wagner and Stauffer 1982). From 1979 to 1984, pink salmon in the Great Lakes exhibited declines and local failures, perhaps due to increased alevin mortality caused by low flow conditions in tributaries during the autumn of 1979 (Bagdovitz et al. 1986; Peck et al. 1994). Some of the streams that contained 10,000 or more spawners in 1979 showed fewer than 200 spawners in 1981 and 1983 (Kocik et al. 1991). In contrast, pink salmon numbers in Canadian tributaries remained relatively high during this period. Pink salmon underwent major increases in Lake Huron and were extremely abundant in the sport catch of 1985 (Nicolette and Spangler 1986; Kocik and Taylor 1987*a*). Kelso and Noltie (1990) argued that conclusions regarding general declines in pink salmon abundance were premature due to contradictory trends in abundance of pink, coho and chinook salmon. Kelso and Noltie (1990) also suggested that populations in Lake Superior (and perhaps all of the Great Lakes) were still in flux, and that it may be more meaningful to examine the biomass sum of anadromous fishes combined, regardless of species. Recent data indicate that pink salmon abundance has declined significantly in Lake Erie and the upper Great Lakes; pink salmon are now only rarely reported in Lake Ontario (Kocik and Jones 1999).

The history of pink salmon in the Great Lakes can be considered both a tremendous failure and a resounding success. Failure in the sense that pink salmon were never intended for introduction by fisheries managers to the Great Lakes. Success in the sense that pink salmon were able to survive, reproduce, migrate and adapt to the Great Lakes ecosystem — without continued human assistance.

The unintentional, yet successful, establishment of pink salmon in the Great Lakes surprised many fisheries biologists who had come to believe that some of the Pacific salmonines (e.g., pink salmon, chinook salmon, coho salmon) required exposure to marine conditions to successfully establish wild populations. Obviously, the establishment and dispersion of pink salmon in Lake Superior proved that this premise was wrong. However, the pink salmon issue did more than pique the curiosity of a few naturalists; it triggered a fundamental shift in the attitudes and plans of Great Lakes fishery managers who were now aware that introduced salmonines could indeed thrive in the Great Lakes.

2.3 Arctic salmonines

2.3.1 Arctic charr (*Salvelinus alpinus*)

The Arctic charr is native to freshwaters on all northern land masses, including North America, Asia, Europe, Iceland and Greenland (Scott and Crossman 1973). Depending on local characteristics of populations, this charr may enter marine environments for feeding, or it may exist entirely in freshwater.

In 1871, a small shipment of Arctic charr was transported from England to Newcastle, Ontario where they were released to a tributary of Lake Ontario (Goode 1882), presumably Wilmot Creek. In 1890, a few Arctic charr imported by the State of Michigan from Switzerland, were released into a tributary that presumably fed either Lake Michigan or Lake Huron (Emery 1985). In 1954 and 1967, Arctic charr were once again introduced to the Great Lakes Basin, in waters of southern Ontario and New York, respectively (Emery 1985). Apparently, none of these attempted introductions succeeded in establishing large or self-sustaining populations of Arctic charr in the Great Lakes drainage basin (Emery 1985).

2.4 Objectives for salmonine introductions to the Great Lakes

It is important to realize that the objectives for Great Lakes salmonine introductions have varied with species, lake, jurisdiction and — most notably, over time. To examine the objectives that have historically been associated with these introductions, I present them in the context of possible objectives (see Li and Moyle 1981, 1993; Kohler and Stanley 1984). I conclude this section with general observations on the patterns in trends of salmonine introductions to the Great Lakes basin from 1870 to the present.

2.4.1 Relocation Objectives

Humans may introduce fish simply to have the fish exist in a particular place, without an associated desire for the fish to satisfy any productive or effective requirements in the receiving ecosystem (MacCrimmon 1977; Li and Moyle 1993). Two subcategories included in this classification would be Aesthetic Objectives and Species Refuge Objectives.

Aesthetic Objectives

Aesthetic Objectives for fish introductions attempt to please humans simply by providing a particular species in a particular setting. While there may have been some cultural association between North Americans of European descent and European salmonines introduced to the Great Lakes (e.g., for example, consider the 'Acclimatisation Societies' of New Zealand described by McDowall 1994), it is unlikely that this was a major objective for any intentional introduction during the recent era. Other than a few general references to the beauty of salmonines (e.g., MacKay 1969; MacCrimmon 1977) or the idea of Atlantic salmon as a 'heritage species' (G. Power, personal communication, 1997), the aesthetic aspect of stocking programs has apparently not been a dominant force in Great Lakes salmonine introductions.

Species Refuge Objectives

Species Refuge Objectives for fish introductions attempt to provide a threatened species with a safe refuge from risk of extinction. Apparently, none of the Great Lakes salmonine introduction programs were intended to provide a safe refuge for a species that was being threatened with extinction in its native range. The only possible exception could have been the Atlantic salmon that were native to Lake Ontario (Section 2.1.1); however, these fish were already extinct long before the recent era of introductions (MacCrimmon 1977).

2.4.2 Harvest Objectives

Humans may introduce a fish to directly satisfy some human demand to retrieve the fish or its offspring in the future. Three kinds of harvest objective would be Food Fisheries Objectives, Commercial Fisheries Objectives and Recreational Fisheries Objectives. According to Kocik and Jones (1999), the primary goal of salmonine introductions to the Great Lakes up to the 1960s was to restore lost fishery production.

Food Fisheries Objectives

Food Fisheries Objectives for fish introductions would attempt to produce harvests of fish for human consumption. While some of the recent introduction programs made reference to the salmonines providing food, this objective was typically expressed as a function of the commercial fishery (MacCrimmon 1977; Mills et al. 1993). Food fisheries, in the strictest sense, were apparently not a major factor in the Great Lakes salmonine introduction programs. Given the modern concerns over bioaccumulation of toxic contaminants in Great Lakes fishes, especially introduced salmonines (e.g., DeVault 1985; Fitchko 1986; Fontaine and Stewart 1992), food production is unlikely to be a major factor in shaping salmonine introduction programs for the Great Lakes.

Commercial Fisheries Objectives

Commercial Fisheries Objectives for fish introductions attempt to produce harvests of fish which may be sold by humans, typically as food items, for money. Several of the Great Lakes salmonine introduction programs implicitly or explicitly stated that these fish might support a commercial fishery, if there was surplus production above and beyond the requirements of the recreational fishery (e.g., Maher 1964; Tody and Tanner 1966). However, experience has shown that commercial fishermen in U.S. waters, and later in Canadian waters, were prohibited from catching and selling salmonines that had been intentionally introduced (Scott and Crossman 1973; MacCrimmon 1977). As a result, it is highly unlikely that Commercial Production Objectives were dominant in Great Lakes salmonine introduction programs. This is supported by the observation that commercial fishermen have generally been opposed to all salmonine introductions (H. Regier, personal communication, 1997)

Recreational Fisheries Objectives

Recreational Fisheries Objectives for fish introductions attempt to produce opportunities for excitement and reward of human leisure activities. This harvest objective has often been related to economic factors, particularly those of supporting tourist industries (MacKay 1969). While wild reproduction has often been an implicit condition associated with the Recreational Production Objective (but see Marcogliese and Casselman 1998), the modern proponents of salmonine angling have apparently been satisfied by put-grow-and-take fisheries:

> *"One tool that fishery managers employ is stocking hatchery reared fish (e.g., Heidinger 1993; McGurrin et al. 1995). Stocking programs sometimes have an explicit goal of rehabilitating or creating self-sustaining population. ... Another goal of stocking programs is to support recreational fisheries on a put-grow-take basis (e.g., Heard et al. 1995; Kinman 1995; Lange et al. 1995). This has been a goal of many stocking programs for Pacific salmon in the Great Lakes. In some cases, stocking programs have both these goals (e.g., Perry 1995)."* (Bence and Smith 1999, p. 299)

2.4.3 Manipulation Objectives

Humans may desire to introduce a fish to indirectly produce some desired change in an aquatic ecosystem. Three such objectives would be Niche Filling Objectives, Forage Supplement Objectives and Biological Control Objectives.

Niche Filling Objectives

Niche Filling Objectives for fish introductions attempt to replace some previously existing, native fish species in an ecosystem. The concept of an 'empty,' 'vacant' or 'free' niche is often cited by proponents of Niche Filling Objectives. According to these interpretations, after the extinction of a community member (e.g., top piscivore) the ecosystem retains a 'vacant niche' that corresponds to the previous ecological characteristics of the extinct member. The proponents claim that this 'vacant niche' continues to be available as a potential role within the community; a role which may be fulfilled by re-introduction of the extinct member or by introduction of a different species. Thus, according to proponents of Niche Filling Objectives, it is desirable to have all of the major roles within the community filled so as to 'maximize' or 'normalize' the structure and function of the community. If the pre-existing native species cannot fully 're-occupy' the 'vacant niche' (e.g., through rehabilitation programs), or if there are additional human benefits attributed to a non-native species such as fisheries enhancement, then a non-native species may be considered a desirable candidate to 'fill the vacant niche.'

The validity of the 'vacant niche' premise has been contested in ecological debates. The first problem has to do with the concept of a species' 'niche.' Early versions of 'niche' were given a variety of meanings, including the description of 'niche' as a property of the environment (see Ricklefs 1979). In 1958, G.E. Hutchinson formally defined a 'niche' as a property of the species, rather than the environment; a property that is measured as the range of the species' activity along abiotic (physico-chemical) and biotic (living) dimensions of the ecosystem — e.g., prey size, prey type, depth of water, water velocity. The 'niche' is described after the fact, so the description refers to only the realized portion of activities, rather than all of the possible activities (Li and Moyle 1981, 1993). According to this ecological theory, it is logically impossible to have a 'niche' which is 'vacant.' When a species is reduced or eliminated from a community, so goes its 'niche' — by definition. The community necessarily responds to the reduction and elimination, and the community takes on a new ecological structure and function. It is possible that the extinguished species may be successfully re-introduced into the community, in which case it would have to forge new ranges of activity along the abiotic and biotic dimensions of the changed ecosystem and establish a new 'niche'. More importantly, a non-native organism introduced into an ecosystem that has been changed by reduction/extinction of a native species, cannot fill a niche because, by definition, it no longer exists. Li and Moyle (1981) argued the introduced species must forge out its own niche.

Niche Filling Objectives have been raised for salmonine introductions to the Great Lakes. For example, fisheries managers spoke of 'replacing' ciscos with kokanee, and other salmonines 'replacing' Atlantic salmon and lake charr (e.g., Christie 1968; Christie et al. 1972). Regier (1968) argued against the Niche Filling Objective for Great Lakes fisheries managers early in the recent era of salmonine introductions:

> *"People who favour the introduction of one or more exotic species may make mention of a "vacant niche" in some community. This idea of a vacant niche is a potentially confusing one. The contemporary connotations of niche derive from Charles Elton's use of it in the sense of the functional status of an organism in its community. Many ecologists now take the niche as a characteristic of the organism and not really of the habitat. But when we use the term "vacant niche" we clearly have a characteristic of the system or of the habitat in mind, else it would in fact mean something like this: an unnamed species that I have in mind normally plays a functional role of a sort that the species could become a significant component in the community under consideration. Though this may well be the way in which some proponents of introduction approach the problem, I doubt that they intend to be so forthright about their approach when they use the term "vacant niche."*
>
> *I think what is often meant by "vacant niche" is that certain possible trophic levels in the community haven't enough organisms in them for the good of the system as a whole. The "good of the system" of course is almost invariably seen in terms of its potential production of what man sees to be an immediate benefit. As an example, one of the major objectives in the State of Michigan's program of introducing exotics in Lake Michigan is to add species to the terminal predator trophic level in order to prey on the alewife and smelt. (Tody and Tanner, 1966)."* (Regier 1968, p. 95)

Thus, we can see that when Great Lakes fisheries managers referred to filling 'vacant niches,' it is possible that they may have been confusing this for some form of Exploitation or other Manipulative Objective (e.g., Recreational Fisheries or Biological Control).

One final comment should be made about the Niche Filling Objectives as they apply to the recent era of salmonine introductions to the Great Lakes. There is some evidence that the introduced salmonines were originally intended by fisheries managers only as a short term replacement predator and sportfish until lake charr were successfully rehabilitated (Herdendorf 1983). For example, consider Wainio's (undated) comments on Pacific salmon in Lake Ontario:

> *"With no large predator remaining, and with a swarming forage fish base developing, there was a need for a fast-growing predator (such as the coho salmon) until a native predator (such as the slow growing lake trout) could recover."* (Wainio undated)

and Kocik and Jones' (1999) general comments on what they call the 'restoration view:'

> *"The restoration view considers the Great Lakes as recovering ecosystems requiring management to restore ecosystem health — primarily through rehabilitation of native species. In this view, lake trout (*Salveliinus namaycush*) are a measure of ecosystem health (Edwards et al. 1990) and Pacific salmonines are temporary components whose prominence is inconsistent with long-term management strategies."* (Kocik and Jones 1999, p. 455)

Forage Supplement Objectives

Forage Supplement Objectives for fish introductions attempt to increase prey availability for a desired fish species existing within an ecosystem.

Given the fact that most salmonines introduced to the Great Lakes are top piscivores as adults, it is highly unlikely that these species were intended to serve as a prey base for some other species. The only possible exception would have been the kokanee, which apparently was intended to serve a 'secondary function' as a forage fish for other (undefined) species in the Great Lakes fish community (MacCrimmon 1977).

Biological Control Objectives

Biological Control Objectives for fish introductions attempt to decrease the abundance of a species considered by humans to be pests or nuisances.

During the recent era of salmonine introductions to the Great Lakes, fisheries managers expressed an urgent need for an open-lake predator to reduce the abundance of alewife and also rainbow smelt:

> *"... the pressing nature of Lake Michigan's fishery problems are evident, spectacularly so when a massive and revolting dieoff of alewives occurs. Hence, the Department of Conservation must try to cope by manipulating nature in the raw, and in the large."* (Carter 1968, p. 555)

and

> *"Alewife were so spectacularly abundant in the mid 1960s, that they repeatedly clogged municipal and industrial water intakes (Greenwood 1970; Wells 1973). During the 1967 die-off, which was thought to involve more than 130,000 t of fish, tons of dead and dying alewives clogged harbors and washed ashore, presenting a difficult and costly cleanup problem. The loss to industries, municipalities, and recreational interests was reportedly in excess of $100 mil-*

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[3] In 1885, European settlers in New York and Michigan attempted to establish wild populations of this maritime (Atlantic) species as a forage base for salmonines (presumably native species) in Great Lakes tributaries (MacCrimmon 1977). From 1906 to 1921, forty million smelt eggs were released in the St. Marys River between Lakes Superior and Huron, to provide forage for the Atlantic salmon that had recently been introduced there (Bower 1909; Creaser 1926). According to MacCrimmon (1977), neither of these stocking programs resulted in the establishment of a self-sustaining population of rainbow smelt. However, in 1912 the State of Michigan intentionally stocked 22 million smelt eggs into Crystal Lake and Torch Lake in the Lake Michigan drainage basin (Van Oosten 1937). During the 1920s and 1930s, wild rainbow smelt were recorded at progressively greater distances from Crystal Lake, providing circumstantial evidence that all of the Great Lakes populations were derived from this stocking (Van Oosten 1937; Mills et al. 1993; Crowder 1986).

> *lion (U.S.) (Greenwood 1970). In response to the 1967 die-off in Lake Michigan, a joint state-federal investigation was undertaken in 1968, with the aim of evaluating methods of reducing the numbers of dead fish washing ashore and removing large numbers of live fish during spawning runs. Skimming nets up to 4,000 ft long were towed on the surface in the open lake to collect dead, floating alewives, while pound nets were set in harbors to remove live alewives (Greenwood 1970).*" (O'Gorman and Stewart 1999, p. 502)

Alewife had invaded the upper Great Lakes as a result of human canal construction, and the rainbow smelt populations had unexpectedly blossomed after straying from their original sites of intentional introduction[3]. Thus, both of these species were themselves the unanticipated and negative side effects of previous human activities.

It should be noted that classical biological control theory is much more sophisticated than simply introducing a species that has the potential to prey upon some other undesirable species (see Huffaker and Messenger 1976 for sources that were available in the 1960s). Classical biological control theory and practices were being used, especially in agricultural situations, prior to the recent era of salmonine introductions to the Great Lakes. These methods originated from the work of scientists who sought to control non-native agricultural pests by introducing an effective predator — typically one that had co-evolved with the pest in its native geographic range. The stringent principles associated with classical biological control were developed with the purpose of minimizing the risks of unplanned and undesirable ecological side effcts.

Evidently, proponents of salmonine introductions for biological control in the Great Lakes did not adopt the existing theory and practices of classical biological control. Great Lakes fisheries managers did not conduct basic ecological studies to determine the risk of unexpected and undesirable consequences of introducing a "generalist vertebrate predator" such as the non-native salmonines.

2.4.4 Historical trends in introduction objectives

Based on the historical information presented in Sections 2.1–2.3 of this report, I have attempted to summarize (Table 3) the various objectives that have been associated (inferred or stated) with the Great Lakes salmonine introductions during the early (1870–1960) or recent (1960–present) eras. There are a few general observations that can be made on the basis of this summarization.

First, it can be seen from Table 3 that the majority of species (i.e., Atlantic salmon, brown trout, chinook salmon, coho salmon, rainbow trout) are common to both early and recent eras. This may reflect the high desirability of salmonines for fisheries related objectives, as well as a generally high similarity among the salmonines with respect to fisheries or ecological objectives.

Second, it can be seen that there were general differences among the categories of introduction objectives. There were hardly any cases in which Relocation Objectives were identified, and these were restricted to aesthetic introductions during the early era. Similarly, for the cases in which ecological Manipulation Objectives (i.e., Biological Control, Forage Supplement) were actually identified, these were proposed only in the recent era. It should be obvious from Table 3 that the vast majority of objectives associated with salmonine introductions to the Great Lakes basin, in both early and recent eras, were directly related to fisheries harvests.

Third, within the Harvest Objectives, it can be seen that introduction objectives changed dramatically between the early and recent eras. During the early era of salmonine introductions, the various harvest objectives applied equally to commercial and recreational fisheries, with a few references to supporting food fisheries as well. However, in the recent era there was an obvious shift away from food and/or commercial fisheries — to a situation where virtually all modern salmonine introductions have had the primary objective of supporting recreational fisheries.

Table 3. Summary of objectives (inferred = ?, stated = ✓) associated with introductions of salmonines to the Great Lakes basin during early (1870–1960) and recent (1960–present) historical eras.

	Objective for introduction							
	Relocation		Harvest			Manipulation		
Species	Aesthetic	Species refuge	Food	Commercial	Recreational	Niche filling	Forage supplement	Biological control
				Early (1870–1960)				
Atlantic salmon			✓	✓	✓			
Brown trout	✓				✓			
Chinook salmon			✓	✓	✓			
Coho salmon				?	?			
Rainbow trout	✓			✓	✓			
Chum salmon				?	?			
Cutthroat trout				?	?			
Masu salmon				?	?			
Arctic charr				?	?			
				Recent (1960–present)				
Atlantic salmon					✓	✓		
Brown trout					✓			
Chinook salmon				?	✓	✓		✓
Coho salmon				?	✓	✓		✓
Rainbow trout					✓			
Kokanee				?	✓	✓	✓	?
Pink salmon				unintentional				
Arctic charr					?			

3

Ecology of salmonine introductions to the Great Lakes

This section focusses on the theory and evidence concerning ecological effects of the various salmonines that have been introduced to the Great Lakes drainage basin. I recognize two general classes of ecological effects that can result from introductions (Weir 1977):

- Effects of introductions on the introduced Great Lakes salmonines
- Effects of introduction on the Great Lakes ecosystems.

While introduced fish species may adversely affect terrestrial ecosystems (Kohler and Stanley 1984), I focus primarily on the structure and function of aquatic ecosystems.

It should be kept in mind that fish introductions have already proven to be ecologically significant elsewhere in the world (Thomson 1922; McDowall 1968, 1978; Vooren 1972; Courtenay et al. 1986; Cowx 1998):

> *"When reviewing the history of fish stocking and introduction around the world, it is clear that there have frequently been catastrophic or at least seriously damaging results, and that rarely — if ever has either stocking or introduction provided the anticipated benefits without large unanticipated negative consequences."* (Hilborn 1999, p. 122)

For a global overview of ecological effects associated with fish introductions, I refer the reader to an international symposium "*The Ecological and Genetic Implications of Fish Introductions (FIN)*" published by the *Canadian Journal of Fisheries and Aquatic Sciences* (Billington and Hebert 1991), with case studies from Africa (Ogutu-Ohwayo and Hecky 1991), Europe (Holik 1991), Australia/New Zealand (Arthington 1991), tropical Asia and America (Fernando 1991) and North America (Moyle 1986; Crossman 1991; Krueger and May 1991). More recent, general investigations and reports on the ecological effects of fish introductions can be found in Flecker and Townsend (1994), Lassuy (1995), FAO (1996), Dill and Cordone (1997), Moyle (1997), Cowx (1998), FAO (1999), Gido and Brown (1999), Nico and Fuller (1999), Whittier and Kincaid (1999), Rahel (2000).

While these global perspectives on fish introductions are important for developing general ecological principles, it is important to remember that the specific effects generated by introductions are largely a reflection of the local circumstances under which they occur:

> *"Many of the impacts of stocking and introduction are very different depending upon the geographic isolation of the target habitats and the history of the region with respect to previous introduction."* (Hilborn 1999, p. 122)

For the purposes of this review, I will attempt to relate the potential ecological effects of salmonine introductions to the specific characteristics of the Laurentian Great Lakes drainage basin, and the life forms that evolved therein.

3.1 Effects of introduction on the introduced Great Lakes salmonines

This section describes the ecological effects of introduction on characteristics of the non-native salmonines that were released into the Great Lakes ecosystem. These characteristics include:

- Survival, growth and development
- Dispersion and migration
- Reproduction
- Alteration of life-history characteristics

This classification of ecological effects arising from introductions is consistent with that adopted by the United Nations' "*Precautionary Approach to Capture Fisheries and Species Introductions*" (FAO 1996, p. 37).

3.1.1 Survival, growth and development

Many fish introductions fail because the fish do not survive in their new environment. Prevailing conditions in the receiving ecosystem may have a singular or combined effect that precludes the introduced fish from maintaining essential physiological processes. The introduced organisms evolved in a different ecosystem, with adaptations to satisfy these requirements; however, the ecosystem into which they are introduced may pose novel threats to the organism's survival.

After reviewing the early history of salmonine introductions to the Great Lakes, it would be safe to say that little return was received from the investment of stocking effort. In general it can be said that the intentionally introduced salmonines often experienced difficulty establishing self-sustaining populations in the Great Lakes; a situation which was often considered by early proponents to be a failure. Ironically, the only introduced salmonine to clearly prove its ability to independently maintain wild populations in the Great Lakes (in the recent era), was the only species that was not intended to establish such populations — that is, the pink salmon.

Why didn't the early salmonine introductions achieve the results desired by the European settlers? Given the large stocking programs of the Americans, it is unlikely that the failures can be simply attributed to insufficient numbers of released fish (Regier and Kay 1996). Although low stocking intensity is commonly blamed for introduction failures, it is a rather limited explanation in both theory and application. Consider that pink salmon established a self-sustaining population in Lake Superior with relatively small numbers of released fish, compared to the intensive stocking of other programs.

Kocik and Jones (1999) suggested that early introduction attempts were thwarted by poor choices of developmental state (e.g., use of adults rather than smolts) and of stocking locations (e.g., warmwater rather than coldwater streams). Christie et al. (1987) suggested that the early community structure of the Great Lakes, in particular the existence of other large fish, somehow prevented establishment of introduced salmonine populations.

It is also possible that the Atlantic and Pacific salmonines selected by the early European settlers were poorly adapted (i.e., maladapted) for survival and/or reproduction in the Great Lakes ecosystem. These non-native salmonines evolved under circumstances which were very different from those found in the Great Lakes (e.g., Teel et al. 2000). That is, they required certain conditions to survive and reproduce in sufficient numbers, and many of these conditions simply were not met by the Great Lakes environment and/or community. Some of the specific factors that could have been responsible for the failure of early introductions include:

- Inappropriate water conditions (no saltwater, high water temperature, high pollution)
- Inappropriate or insufficient spawning habitat (short river runs with bedrock, clay or mud substrate)
- Inappropriate primary and secondary production (too little or too much energy production)

For coho salmon and kokanee, the ability of the fish to actually survive in the Great Lakes appeared to have been quite limited. For brown trout and chinook salmon, the fish seemed to survive reasonably well but they often failed to successfully reproduce in numbers large enough to develop self-sustaining populations.

The failure of early introduced salmonines to adapt to the Great Lakes led to termination of most stocking programs by 1960. Although the termination of these stocking programs was not well documented, it is likely that these decisions were made more for economic than ecological reasons.

During most of the recent era, many of the introduced salmonines stocked in the Great Lakes seemed to exhibit relatively high adult survival rates. Osmoregulation of the marine salmonines was expected to be a problem; however, survival in freshwater was actually much higher than expected. Most of the open-lake introduced salmonines found an abundant food source in the alewife and rainbow smelt populations, as anticipated by proponents of the introductions. This abundance of prey is considered a major factor underlying the fast growth rates observed in the lakes.

Growth is typically slower in Great Lakes tributaries, compared to growth in the open-lake environments (Taube 1976). For those species that can reside in rivers and streams for extended periods (i.e., rainbow and brown trout), a combination of available habitat and prey likely limited both their abundance and growth (Christie 1968). However, in some cases introduced salmonine juveniles (e.g., rainbow trout) have been observed to grow rapidly in Great Lake nursery streams (Stauffer 1972).

Investigators have also discussed the possibility that environmental factors may have caused problems with egg viability and embryonic/juvenile survival — for example in coho salmon (Johnson and Pecor 1969; Morrison et al. 1985), chinook salmon (Skea et al. 1985) and steelhead (Skea et al. 1985). Chinook and coho salmon juveniles are also vulnerable to EMS = 'early mortality syndrome,' a physiological condition associated with thiamine deficiency during early development (Honeyfield et al. 1998; Ketola et al. 2000).

In some cases, a relatively large percent of introduced salmonines survive from stocking to some point in their life history. Rates of overwinter survival by juvenile coho salmon in Lake Superior streams were actually found to be significantly higher than survival estimates from their native Pacific range (Ford 1997). However, it should be noted that post-juvenile survival in these same Great Lakes tributaries was significantly lower than in their native range, perhaps due to physiological stress or intense predation (Ford and Lonzarich 2000). Savitz et al. (1993) estimated that approximately 8% of stocked chinook and coho salmon returned on spawning runs. According to Parsons (1973) recovery rates for coho salmon stocked in the mid-1960s ranged from 1–21% for the different lakes (Ontario 1%, Superior 6%, Erie 8%, Huron 17%, Michigan 21%). Survival of chinook salmon in Lake Michigan from stocking to spawning run has been estimated at 7–9% (Rybicki 1973). Kitchell and Hewett (1987) reported that returns to the Lake Michigan chinook sport fishery was approximately 10% of the salmon stocked. Lake Ontario's sport fishery for introduced salmonines has waned over the past decade, and this decline has been interpreted as a reflection of decreased survival of hatchery fish in the lake (Savoie and Mathers 1994).

Rand and Stewart (1998*b*) found that modelled survival rates for hatchery chinook salmon in Lake Ontario (11–14% for the period smolt to spawning adult), were similar to those reported by Stewart et al. (1981) for Lake Michigan chinook salmon. Rand and Stewart (1998*b*) also noted that these survival rates from the Great Lakes were approximately an order of magnitude greater than those reported for hatchery and wild chinook salmon from the Pacific coast. The authors suggested that elevated survival in the Great Lakes may be explained by the lack of natural predators that co-evolved with the salmon in their native range:

> *"We did find that our estimated survival rates for hatchery chinook salmon in Lake Ontario (11–14% smolt — spawning adult survival) were similar to those reported for Lake Michigan chinook salmon (Stewart et al. 1981). These values for chinook salmon survival in the Great Lakes are approximately an order of magnitude larger than that reported for wild and hatchery chinook salmon in the Pacific Ocean (1–2% smolt — spawning adult survival: Cross et al. 1991; Bradford 1995). It is not clear what is the cause for this difference, but it may be due to depressed predation rates on juvenile chinook salmon in the Great Lakes relative to the Pacific coast. We presume that a Pacific predator community that has evolved sympatrically with salmon could impart a higher mortality on smolts than the existing predator community in the Great Lakes. The relatively high survival rates for chinook salmon in Lake Ontario have contributed greatly to the dramatic increases in predation and production rates that we report in this paper." (Rand and Stewart 1998b, p. 24)*

It is ironic that even in a situation where survival rates were so high compared to their native range, intentionally-introduced salmonines should still exhibit such difficulties in the establishment of self-sustaining populations.

Recent declines in growth rates, condition factors and survival of Pacific salmonines have been reported in Lake Superior (Ford and Lonzarich 2000), Lake Michigan (Berg 1978; Stewart and Ibarra 1991), Lake Huron (LHMU 1998) and Lake Ontario (Jones et al. 1992; Rand et al. 1994; O'Gorman et al. 1997). Many Lake Michigan salmonines have experienced reductions in growth rates and hatchery returns. Also, there have been declines in the average weight of sport-caught chinook salmon since the early 1980's (Stewart and Ibarra 1991; see also LHMU 1998). Compensatory increases in daily ration (to compensate for reduced alewife condition) by Lake Ontario chinook salmon necessitated a related increase in foraging that may have manifested itself in reduced condition and, perhaps, in higher susceptibility to diseases such as bacterial kidney disease or furunculosis (Rand et al. 1994; see also Wesley 1996). Rand et al. (1994) found that percent lipids in standard fillets of brown trout and coho salmon from Lake Ontario (1977–1991) showed that the condition of salmonine predators declined steadily during the 1980s. Rand and Stewart (1998*a*) reported evidence of increased age at maturity in Lake Ontario chinook salmon, suggesting that this observation may be a consequence of prolonged declines in annual growth rates and condition. Seelbach (1993) commented on low steelhead survival rates to spawning, ranging between 1–5%. Recently in Lake Ontario, investigators have discovered unusually high numbers of dead salmon found in bottom trawls (Jones et al. 1992).

Declines in growth rates of introduced salmonines, and associated reductions in survival, have been linked to changes in the carrying capacity of the receiving ecosystem to support top-level predators:

> *"If prey alternatives to alewife are not sufficiently abundant when and where the salmon need them, slower growth could translate into stress, disease, and mortality." (Stewart and Ibarra 1991, p. 920)*
>
> *"Dramatic declines in commercial and recreational fisheries for coho salmon (Oncorhnychus kisutch) in Lake Superior have raised questions about the natural factors that limit their productivity." (Ford and Lonzarich 2000, p. 94)*

After 30 years of intensive salmonine introductions, alewife, rainbow smelt and Pacific salmonines have declined substantially in Lake Superior, while lake charr have recovered to where the introduced salmonines currently make up less that 10% of the salmonine catch lakewide (Hansen 1994; Ford and Lonzarich 2000). It is possible, as suggested by Kelso and Noltie (1990), that it is the sum of salmonine biomass that is key to understanding changes in abundance, while a particular species' contribution to a stable biomass may fluctuate over time. Nonetheless, alewife and rainbow smelt are declining in the other Great Lakes as well (Brown et al. 1987; Henderson and Nepszy 1989; Jones et al. 1993), and it has been predicted that the situation observed in Lake Superior may be repeated elsewhere in the near future (Stewart and Ibarra 1991; Eshenroder et al. 1995; Regier and Kay 1996; LHMU 1998).

These changes in the growth and survival of introduced salmonines have resulted in reduced economic returns to the recreational fishery, discontent among anglers who favour introduced over native species (Huggler 1989) and pressure to compensate by increasing stocking rates (Keller et al. 1989).

3.1.2 Dispersion and migration

Given that an introduced organism's habitat requirements change throughout its life-history, fish will likely need to move away from the release location to survive. The influence of the receiving ecosystem on dispersion and migration of the introduced species may be substantial. Dispersal and migration potential of introduced species are often overlooked or underestimated by proponents of an introduction (Li and Moyle 1981). Introduced species can also take advantage of connected water courses as they invade new waters far from the intended site of introduction.

Most of the salmonines introduced to the Great Lakes were known to be highly dispersive in their native range (Scott and Crossman 1973). Ironically, there appears to have been little concern expressed by Great Lakes fisheries managers over dispersion and migration of introduced salmonines in their new environment. Recently, however, some researchers have made explicit reference to these kinds of concerns:

> *"Because the Great Lakes drain to the Atlantic Ocean, the ethics of causing the establishment of Oncorhynchus downstream where they may not be wanted is also an issue. Dumont et al. (1988) appropriately questioned the propriety of these introductions made without the consent of the Province of Quebec or other potentially affected jurisdictions." (Eshenroder et al. 1995, p. 524)*

The following text examines the evidence that has been reported for dispersion and migration of introduced salmonines in the Great Lakes drainage basin.

Dispersion

Investigations on brown trout stream movement have indicated that populations exhibit some degree of spatial stability in which individuals often remain in a limited area for several weeks or months (e.g., Schuck 1945). In a long-term study of brown trout dispersion, Shetter (1968) found that many individuals within a population moved very little over a period of several years. Evidence of distinct brown trout populations, between and within tributaries in Lake Superior (Krueger and May 1987*a*) and Lake Huron (Favro et al. 1986), showed little instream dispersion. It has been proposed that this form of spatial stability in stream trout populations may be a result of territoriality or dominance hierarchies (Mense 1975).

When stream-resident brown trout move several kilometres, it is typically larger individuals which apparently require more living space and/or food (Shetter 1968). In contrast, Meyers et al. (1992) investigated stream movements by brown trout in Beaver Creek (Lake Michigan) where they found that while many individuals were rather sedentary during winter and summer, some were quite mobile (7–20 km) during spring and autumn. Clapp et al. (1990) reported that large brown trout in the Au Sable River system (Lake Huron) moved in autumn, and spent the winter in stream segments that were considered to be 'marginal' summer trout habitat. These investigators reported upstream and downstream movements ranging from 33 to 370 km.

Stream-resident rainbow trout apparently do not disperse greatly. Cargill (1980) reported little movement of rainbows in a Minnesota stream which drains to the Mississippi. Shetter (1967) reported little dispersion of rainbow trout that were experimentally-planted in a Michigan tributary that supported a dense population of brook charr. Steelhead juveniles stocked in Lake Superior tributaries showed little instream dispersion (Close and Anderson 1992). Dodge (1972) reported that the vast majority (>95%) of adult rainbow trout tagged in three Owen Sound (Lake Huron) tributaries were recaptured within 8 km of the capture streams. Evidence of distinct rainbow trout populations (Krueger and May 1987*b*) is consistent with the idea that stream-resident rainbow trout do not typically disperse great distances in Great Lakes tributaries. However, it should be noted that even land-locked forms, including some strains of rainbow trout, have been known to revert to a migratory existence, even after thousands of years of geographic isolation (Foerster 1947; Scott and Crossman 1973).

Within open waters of the Great Lakes, most introduced salmonines exhibit high degrees of dispersion, both within and between basins (MacKay 1969). Behmer et al. (1993) reported extensive dispersion of Atlantic salmon recently stocked into the St. Marys River. Brown trout typically use streams for their entire life-history, however some lake-run populations are known to exist (MacCrimmon and Marshall 1968; Kocik and Taylor 1995). Evidence of extensive within-basin brown trout movement has also been reported for Lake Ontario (Haynes and Nettles 1983) and Lake Erie

(Wenger et al. 1985). Dispersal by brown trout in Lake Ontario appears to be related to prevailing water currents (Niemuth 1967; Nettles et al. 1987).

Even strains of the rainbow trout, a species which is not characterized by extensive instream dispersion, exhibit remarkable movement in open Great Lakes environments:

> *"The introduction of the anadromous steelhead into the Great Lakes has resulted in some prodigious journeys. One fish, taken in the Bay of Quinte, Lake Ontario, in January, 1958, had been part of a tagged group released in Great Lakes rivers in Michigan. From release to capture, a period of 8 months, it had travelled about 600 miles, survived a descent of Niagara Falls (unless it negotiated the Welland Ship Canal), and grew 10 inches (254 mm) in length." (Scott and Crossman 1973, p. 189)*

Movements of rainbow trout in open Great Lakes environments have generally been brief, but are often rapid and wide-ranging (Winter 1976; Wenger 1982; Kelso and Kwain 1984; Wenger et al. 1985). Haynes et al. (1986) suggested that this dispersal behaviour was similar to that observed by rainbow trout in their native Pacific Ocean. Skamania stocked by the State of Michigan have been reported in the Saugeen River watershed in Ontario (Smith 1991). Evidence from radio-tagged rainbow trout in Lake Ontario showed extensive dispersion, especially movements suspected to be associated with seasonal formation and movement of the thermocline (Haynes et al. 1986). Hansen and Stauffer (1971) reported that rainbow trout dispersal within U.S. waters of the upper Great Lakes was not extensive, however several of their tagged individuals were observed to move from Lake Huron to Lake Erie and Lake Ontario.

From the beginning of recent introductions, coho and chinook salmon were expected to disperse widely in the Great Lakes:

> *"It can be expected that coho will disperse over large areas in the Great Lakes. Dispersal will be influenced by temperature, water conditions, and the availability of food. Some coho may migrate from one Great Lake to another or even attempt to migrate to the sea." (Tody and Tanner 1966, p. 21)*

In fact, intra-basin movement has been quite common, especially for chinook and coho salmon in Lakes Michigan and Ontario (MacKay 1969; Scott and Crossman 1973). Within 2 years of the 1966–67 coho salmon releases in Lakes Superior, Huron and Michigan, Canadian anglers began catching the animals in the waters of Georgian Bay and the north shore of Lake Erie. (Scott and Crossman 1973; MacCrimmon 1977). Haynes and Keleher (1986) reported that chinook and coho salmon in Lake Ontario travelled an average of 4.0 km per day during spring and summer. Hatchery-reared chinook and coho salmon have also been reported to move extensively throughout Lake Superior as they mix extensively with wild fish (Peck 1970; LHMU 1998; Peck et al. 1999). Radio-telemetry studies of chinook and coho salmon have indicated the occurrence of basin-wide movements in both Lake Erie (Wenger et al. 1984) and Lake Ontario (Keleher et al. 1985).

Migration

Rainbow trout typically spend the first 3 years in riverine habitats before migrating to larger and more open lake habitats (MacKay 1969; Biette et al. 1981). Similar migration patterns are exhibited by most introduced salmonines in the Great

Lakes, with the exception of brown trout and rainbow trout which often remain entirely in the tributaries (MacCrimmon 1977). Seasonal in-river migrations of brown trout have been reported to exceed 100 km (e.g., Jensen 1968; Jonsson 1985), especially when associated with autumn spawning and seasonal changes in water temperature or ice conditions (Avery 1983; Haynes and Nettles 1983). Migrations of rainbow trout within tributaries, and between tributaries and open-lake environments, have also been observed (Berst and Wainio 1967).

There is also evidence for migration by introduced salmonines at the level of whole lake basins:

> *"Investigations in 1970 showed that coho salmon migrated around the lake basin in a clockwise direction. In early spring, large numbers of coho were in the Western basin and western part of the Central basin and during the summer months moved along the north shore. By autumn, most migrating adults returned to their planting sites on the south shore but some attempted to spawn in northshore streams in the Eastern basin (R. Scholl personal communication)." (Leach and Nepszy 1976, p. 633)*

Kocik and Taylor (1987*a*) reported northward migration of pink salmon in western Lake Huron, from the St. Clair River in late spring to the Mackinac Straits by late summer. Chinook and coho salmon in Lake Michigan and Lake Huron have both been reported to undertake season migrations around the basin, including some degree of homing during spawning migrations (Bence and Smith 1999).

Prior to the spawning season, introduced salmonines in the open-lakes migrate toward tributaries in which they run *en masse*. In some cases, fish may undertake a spawning migration through open-lake waters where they typically do not reside. Kelso and Collins (1984) reported pink salmon spawning runs through sections of the Lake Huron North Channel which apparently did not hold a resident population of this species.

The degree to which introduced salmonines exhibit homing tendencies during their spawning migrations varies substantially. Stauffer (1972) demonstrated that at least 84% of the autumn spawning run and 66% of the spring spawning run of rainbow trout in the Black River (Lake Michigan) were returning. Winter (1976) radio-tagged autumn-run rainbow trout along Minnesota's shore of Lake Superior, and found that approximately 90% of these fish left the streams during autumn–winter and returned to the same streams the following spring. Seelbach (1993) also reported strong homing tendencies in Lake Michigan steelhead.

In contrast, several investigators have provided evidence of straying during spawning migrations (Scott and Crossman 1973; Patriarche 1980). Straying has been documented in brown trout (Harvey 1991), coho salmon (Peck 1970) and pink salmon (Kwain and Rose 1986) in Lake Superior, as well as chinook and coho salmon in Lake Michigan (Savitz et al. 1993) and kokanee in Lake Huron (Collins 1971). In another of his experiments, Winter (1976) conducted a tag-displacement experiment with rainbows in which no trout returned to the stream of tagging. Winter postulated that the lack of homing among the displaced fish may have resulted from one or more of the following possibilities (see also Biette et al. 1981):

1. stream of initial capture was not the home stream,
2. angler capture (sampling) prevented return to home stream,

3. favourable stream conditions outweighed homing tendency,
4. lack of imprinting,
5. returning adults may have had difficulty distinguishing natal stream because of close proximity (effectively regional rather than stream imprinting)

3.1.3 Reproduction

Even if an introduced species survives, there is no guarantee that it will be able to establish self-sustaining, wild-reproducing (i.e., sometimes referred to as "*naturalized*") populations. The prevailing conditions of the receiving ecosystem may preclude one or more of the following essential requirements for successful reproduction:

- allocation of sufficient energy for reproductive organs and gametes
- location of appropriate spawning habitat
- location of potential mates
- spawning and production of viable offspring

In many cases of fish introductions, the species may survive and disperse in the new ecosystem, yet fail to reproduce in numbers sufficient to support a wild population. In such cases, proponents of the introduction typically abandon their plans or accept the requirement to artificially maintain the population through continued stocking.

Wild reproduction by introduced salmonines in the Great Lakes is highly variable, depending on lake basin, species and local environmental characteristics. Although much talked about in qualitative terms, abundance of introduced salmonines has rarely been quantitatively estimated by Great Lakes fisheries managers (Seelbach 1985; Eck and Wells 1987; Seelbach and Whelan 1988; Kocik and Jones 1999). In many instances, fisheries managers hold the implicit assumption that some aspect of spawning is a "*primary factor limiting fishery productivity*" (Bence and Smith 1999); these assumptions often reflect wishful thinking more than reality.

In some cases, the agency responsible for introductions simply admits to its lack of knowledge about reproduction of introduced salmonines. For example, consider these references to brown trout and chinook salmon in southwestern Ontario tributaries:

> *"Brown trout have been stocked by the Ministry for the purposes of rehabilitation, supplemental introductions and put-and-delayed-take. Stocking which occurs in rivers of the [Owen Sound] District provides a fishery in Owen Sound and in Lake Huron near Kincardine. The purpose of this stocking program is to diversify the fishery. Although the intent is to establish self-sustaining runs of fish, little information exists to indicate if this is happening." (Smith 1991, p. 25)*

> *"Chinook salmon spawn successfully in many streams of the [Owen Sound] District. The contribution to the fishery from naturally reproducing versus stocked fish cannot be measured since no fish were marked. A representative sample of fish will be marked with coded wire tags in 1991 and 1992 to provide this information. ... The combination of fish being produced naturally and those coming from stocking programs leads to uncertainty about the actual size of this*

> *population and the impact these fish may be having on the entire fish community, particularly the forage base." (Smith 1991, p. 31)*

Typically, fisheries ecologists recognize the lack of quantitative information on wild reproduction. In their analysis of Lake Michigan production, Stewart and Ibarra (1991) did not include wild-reproducing introduced salmonines because there was insufficient data on the contribution of wild-reproduction to the populations at large. MacCallum and Selgeby (1987) and LHMU (1998) both indicated that the amounts of wild reproduction exhibited by introduced salmonines in Lakes Superior and Huron (respectively) were unknown, but they believed them to be quite large. Others have tended to accept the hypotheses of self-sustaining reproduction by chinook salmon, coho salmon and rainbow trout in Lake Superior and presented these assumptions as established, yet largely unsubstantiated, facts (e.g., Mason et al. 1998; Bence and Smith 1999).

In contrast, others have indicated that the amount of wild reproduction for introduced salmonines in Lakes Ontario and Erie was unknown, yet they believed it to be small (Hartman 1972; Elrod et al. 1995; Lange and Smith 1995). Some Great Lakes fisheries managers have assumed that, since wild reproduction is often low, population abundance for introduced salmonines is largely explained by changes in hatchery stocking levels and the level of harvest. For example, with reference to Lake Michigan:

> *"Some of the [introduced] salmonines reproduced naturally to varying degrees, but their populations were maintained mainly by stocking. The salmonine populations that have resulted from the plantings have generally not been measured directly, but their trends in abundance should follow, at least roughly, the trends in annual stocking rates."* (Eck and Wells 1987, p. 55)

and for Lake Ontario:

> *"The proportions of wild and hatchery rainbow trout in a stocked and naturally reproducing population are largely unknown because not all hatchery fish are marked (clipped) before they are released (Lake Ontario Fisheries Unit 1986). ... Natural recruitment occurs in tributaries along the north shore of Lake Ontario (M.L. Jones, Ontario Ministry of Natural Resources, personal communication) but is unmeasured."* (Marcogliese and Casselman 1998, p. 253)

The point here is that, on the whole, Great Lakes fisheries managers actually have little if any knowledge about wild reproduction in most populations of introduced salmonines. This is especially true for populations which are annually supplemented by hatchery stocking programs to achieve some target abundance to support the recreational fisheries. Interestingly enough, pink salmon — a species which is not continually stocked — is one of the few species which is definitely known to endure fluctuations in reproduction, yet sustain wild populations (Schumacher and Eddy 1960; MacCallum and Selgeby 1987; Kelso and Noltie 1990; Kocik et al. 1991). For these reasons, the following discussion will focus mostly on qualitative statements made in the literature about levels of wild reproduction of the various introduced Great Lakes salmonines.

Brown trout have established self-sustaining populations throughout the Great Lakes for over 100 years (MacCrimmon and Marshall 1968; Kocik and Taylor 1995; 1996). There are several published references to self-sustaining populations of brown trout in the Great Lakes drainage basin, including: New York tributaries to Lake Ontario (Johnson 1981; Engstrom-Heg and Hurlbert 1983; Preall and Ringler 1989), Michigan and Ontario tributaries to Lake Huron (Shetter and Alexander 1966; Marshall and MacCrimmon 1970), a variety of tributaries to Lake Michigan (Kocik and Taylor 1995) and U.S. tributaries to Lake Superior (Brynildson and Brynildson 1967; Newman and Waters 1989). The apparent success of brown trout reproduction may be due, in part, to the iteroparous (repeat spawning) nature of Atlantic salmonines as opposed to the typically semelparous (single spawning) nature of Pacific salmonines (Scott and Crossman 1973; but see Unwin et al. 1999). Despite the varied reports of brown trout establishment, there are numerous cases in which stocking programs have failed to develop self-sustaining populations. For example, Haynes and Nettles (1983) reported that while there was some evidence of limited reproduction by brown trout in Canadian tributaries of Lake Ontario, there was no evidence of such reproduction along the south shore of the lake. Abraham (1980) reported that wild reproduction of brown trout stocked along the south shore of Lake Ontario was largely unsuccessful, necessitating intensive stocking to support the populations. Kocik and Taylor (1995) made reference to a general decline in brown trout populations in several tributaries to Lake Michigan in the early 1980s. As a general rule, it would appear that introduced brown trout exhibit relatively low, but steady levels of wild reproduction in the Great Lakes (MacKay 1969; Scott and Crossman 1973).

Chinook salmon exhibited successful wild reproduction after the mid-1960s introduction efforts; including the strong 1973 year-class in Lake Michigan (Taube 1974; Rybicki 1973). In some cases, chinook reproduction was reported to occur at substantial levels. Carl's (1982) work on Lake Michigan chinook salmon showed that over 20% of the total estimated smolt population originated from wild reproduction in 1979. Zaft (1992) assessed production of chinook salmon in the Pere Marquette River (Lake Michigan) from 1988 to 1990 and found that smolt production ranged from 52,000 to 100,000 fish per year. Elliott (1994) estimated that wild production accounted for 45–66% of chinook populations in the northeast basin of Lake Michigan and 27–37% in the southeast basin. Self-sustaining populations of chinook salmon have been claimed to be established in Lake Michigan (Hesse 1994; Weeder 1997) and Lake Superior (Peck 1996; Peck et al. 1994; 1999).

Elsewhere, chinook salmon have been reported to exhibit much lower levels of wild reproduction, including: eastern Lake Ontario (Johnson 1978, 1980; Johnson and Ringler 1981; Rand et al. 1992); and all three of the Lake Huron basins (Powell and Miller 1990; Smith 1991). Relatively low contributions from wild reproduction have been noted in Lakes Superior, Huron and Ontario (Berg 1978; Johnson 1978; Borgeson 1981; Johnson and Ringler 1981; Peck 1996). In Lake Michigan, numbers of spawning chinook returning to tributaries began to decline about 1985, and by 1988 may have been 40–50% lower than in the early 1980's (Stewart and Ibarra 1991). In some populations, chinook salmon would not have continued to exist without ongoing stocking of hatchery juveniles (Avery 1974; Patriarche 1980; Emery 1985). Relative to rainbow trout, and perhaps brown trout, chinook salmon certainly do not seem to be as likely to establish and maintain self-sustaining populations in the Great Lakes drainage basin.

Coho salmon, like chinook salmon, have a variable record of wild reproduction in the Great Lakes basin. Evidence of wild reproduction by coho salmon has been reported for Lakes Superior (Peck 1970; Healy and Lonzarich 2000; Ford and Lonzarich 2000), Michigan (Rybicki 1973; Taube 1974; Stauffer 1976) and Ontario (Johnson 1978, 1980; Johnson and Ringler 1981; Rand et al. 1992). In Lake Superior waters near Marquette, Michigan, approximately 94% of the coho salmon sport catch consisted of naturally spawned fish (Peck 1992). Estimates of wild coho salmon contribution to the sport harvest in Lake Ontario have reached as high as 50% (Kocik and Jones 1999). Seelbach (1985) reported the production of 253 coho smolts per hectare in a Lake Michigan tributary where attempts were made to exclude spawners, while Seelbach and Miller (1993) reported coho salmon smolt production as high as 573 smolts per hectare. Notwithstanding these reports of wild coho salmon reproduction, it appears that such reproduction often contributes only a small fraction of the total coho salmon populations:

> *"Coho salmon spawn successfully in nearly all coldwater tributaries of Lakes Michigan, Superior and Huron. Despite this potential for natural reproduction, the total contribution of smolts from natural reproduction was small (6% in the fall of 1979). There appears to be little chance that natural reproduction will be extensive in tributaries of Lakes Erie and Ontario (Parsons 1973)."* (OMNR 1988, p. 15)

and

> *"Although [coho] have established modest self-sustaining populations in numerous tributary systems, population levels in [the upper Great Lakes] stem almost entirely from hatchery stocking."* (Borgeson 1981, p. 1467)

In Lake Michigan during 1979, Patriarche (1980) estimated that only 9% of adult coho salmon caught were the result of wild reproduction. Avery (1974) found only modest reproduction of coho salmon in Little Scarboro Creek, a tributary of the Kewaunee River (Lake Michigan). O'Gorman et al. (1987) stated that while there was evidence of some wild reproduction of coho salmon in Lake Ontario, they considered the contribution of such reproduction to be small because few tributaries were suitable for successful spawning. Once again, we are confronted with the task of separating the contribution of wild reproduction from that of hatchery stocking — and once again, we have little or no scientific data with which to work.

Rainbow trout, along with brown trout to a lesser degree, have been cited as the most successful introduced salmonine in the Great Lakes basin (MacCrimmon and Marshall 1968; Biette et al. 1981; Krueger and May 1987; Seelbach 1993; Krueger et al. 1994; Kocik and Taylor 1996). Rand et al. (1993) estimated that wild steelhead smolt contribution to populations in Lakes Michigan and Ontario ranged from 6–44% and 18–33%, respectively. In seven Michigan tributaries to Lake Michigan, wild rainbow trout comprised 100% of the population in unstocked rivers, 93% in stocked rivers and 60% in two stocked marginal rivers (Seelbach and Whelan 1988). Christie (1972) suggested that early plantings (ca. 1940s) of rainbow trout in Lake Ontario tributaries abruptly expanded to produce established stocks during the following two decades. Once again, the apparent success of rainbow trout in establishing self-sustaining populations may be due in part to its tendency for iteroparity, which stands out from the semelparity typical of most other Pacific salmonines (Kwain 1971; Unwin et al. 1999). Seelbach (1993) found that more than 25% of spawning rainbow trout examined in a population were repeat spawners. There is reported evidence of wild rainbow trout reproduction in all of the Great Lakes (MacCrimmon and Gots

1972) including tributaries of Lake Ontario (Hartman 1972; Johnson 1978, 1980, 1981; Johnson and Ringler 1981), Lake Huron and Georgian Bay (Berst and Wainio 1967; Dodge and MacCrimmon 1970; Marshall and MacCrimmon 1970; Hansen and Stauffer 1971), Lake Michigan (Borgeson 1981; Seelbach 1986; Seelbach and Whelan 1988) and Lake Superior (Bidgood and Berst 1967; Kwain 1981; Krueger et al. 1994; Peck et al. 1994; Negus 1999).

Genetic evidence suggests that some rainbow trout have formed populations that are moving toward reproductive distinction (Krueger et al. 1994). However in contrast to these cases of self-sustaining rainbow trout populations, there are some instances where the rainbow trout seem to be at a disadvantage (see Negus 1999). For example, rainbow trout populations in Lake Michigan may be maintained predominantly by annual stocking of hatchery-reared fish because the tributaries cannot support sufficient wild reproduction (Avery 1974; Scholz et al. 1978). Avery (1974) found only modest reproduction of rainbow trout in Little Scarboro Creek, a tributary of the Kewaunee River flowing into Lake Michigan. Evidently, there have been no reports of successful reproduction by skamania summer-run steelhead (Rand et al. 1993). More recently, Dueck and Danzmann (1996) made references to a general decline in rainbow trout reproduction success in Great Lakes environments.

There are several possible reasons for the reproductive difficulties experienced generally by introduced salmonines in the Great Lakes. For example, consider Hartman's (1973) evaluation of salmonine reproduction in Lake Erie:

> "*Although various salmonids have been introduced ... into Lake Erie since 1870, no important naturally reproducing populations have developed. Apparently one or more of the following factors were responsible:*
>
> - *too few fish*
> - *fish of poor quality*
> - *fish of the wrong size (i.e., developmental state)*
> - *fish lacking home-stream imprinting*
> - *fish planted at the wrong site*
> - *fish planted at the wrong depth*
> - *fish planted in the wrong season.*" (Hartman 1973, p. 35 paraphrased list)

But what is it that would make the Great Lakes such a poor place for non-native salmonine reproduction? Several authors suggest that access to appropriate and sufficient spawning habitat is a principal limiting factor for wild reproduction (see MacKay 1969). For example:

> "*The principal ecological factors limiting the establishment of naturalized populations in Ontario waters of the Great Lakes would seem to be not only the availability of suitable river spawning grounds, but access to suitable breeding areas now blocked by pollution, dams and waterfalls.*" (MacCrimmon 1977, p. 39)

In Lake Michigan, the sport salmon fishery is largely supported by an extensive stocking program; all substantial reports of wild reproduction are limited to the eastern tributaries "*where migrating salmon have access to suitable stretches of streams and rivers*" (Bence and Smith 1999, p. 268, my emphasis).

Several researchers have found that the distribution and abundance of Pacific salmonines spawning in their native range were closely associated with stream channel characteristics including substrate composition and channel bed mobility (e.g., DeVries 1997; Montgomery et al. 1999). If this is generally true, then fundamental differences in Great Lakes tributary geomorphology could preclude the establishment of self-sustaining populations of introduced salmonines. Consider the case of introduced coho salmon in Lake Superior, where juveniles occupy streams characterized by low flow rates in winter, spring flooding and other hydrologic conditions that are quite different from spawning tributaries in their native range:

> *"Unlike in their native range of the Pacific coast, Lake Superior coho salmon juveniles inhabit streams characterized by low winter flows and highly variable summer flows. Because high stream flows can profoundly affect fish behavior and distribution, we hypothesized that the winter ecology of coho salmon in Lake Superior streams would differ from patterns described for Pacific coast populations. Snorkeling surveys completed in winter 1998 examined the distribution and social organization of overwintering coho salmon in simple and complex pools of a Lake Superior tributary in Wisconsin. In both habitat types, coho salmon occupied focal positions in the main channel; however, fish were more tightly distributed and closer to the streambanks in simple pools. Aggressive interactions also were more common in simple pools. These results contrast sharply with research findings from Pacific coast streams, which generally show juvenile coho salmon moving to protected habitats and becoming less aggressive in winter."* (Healy and Lonzarich 2000, p. 866)

It is tough enough for Atlantic and Pacific salmonines to maintain necessary levels of reproduction in habitats where they had evolved, much less in the Great Lakes.

For tributaries of Lake Michigan, limited gravel spawning habitat may often constrain wild reproduction of introduced salmonines (Stewart et al. 1981; Seelbach 1993; Stoffle et al. 1987). Apparently, most of Wisconsin's tributaries to Lake Michigan are poorly suited for salmonine reproduction due to a lack of suitable gravel substrates for spawning, cold winter water temperatures, and large water level fluctuations (Avery 1974; Hansen et al. 1990). Salmonine spawning streams on the west coast of North America typically have higher gradients and are much less productive than streams in the Great Lakes drainage basin (Sheppard and Johnson 1985; Kocik and Taylor 1996). Smith (1991) stated that spawning success by rainbow trout in southwestern Georgian Bay (Lake Huron) was limited by the availability of both spawning and nursery areas. Nicolette and Spangler (1986) concluded that natural barriers to fish passage on the majority of Minnesota tributaries to Lake Superior limited the amount of spawning habitat accessible for anadromous salmonines such as pink salmon, and was the major limiting factor for these populations. Savitz et al. (1993) described a situation where salmon planted by the Illinois Department of Conservation were released in boat harbors because no permanent rivers or streams flow from Illinois into Lake Michigan — the State of Illinois has no appropriate spawning or nursery habitat at all.

Alternative explanations for low levels of wild reproduction by introduced salmonines have also been presented. Stauffer (1976) suggested that insufficient food could affect coho salmon in the Great Lakes by reducing the quantity and/or quality of eggs, thereby affecting the probability of successful reproduction (see also Taube 1976). It should also be noted that large spawning runs and observations of mating do not necessarily indicate high levels of wild reproduction. For example, MacCrimmon and Gordon (1981) estimated a loss of more than 75% of deposited ova due to redd disruption, superimposition and sedimentation. Taken together, factors other than limited spawning habitat may also explain low levels of wild reproduction by introduced salmonines in the Great Lakes.

Would populations of intentionally introduced salmonines in the Great Lakes persist if the stocking programs were terminated? Any answer to this question is highly uncertain, especially since we know so little about the actual levels of their wild reproduction in the Great Lakes. Some fisheries managers have suggested that wild reproduction occurs at such a level that the introductions are "irrevocable" (e.g., Peck et al. 1999). However, based on the available evidence it would appear that many populations of species such as chinook and coho salmon would face an immediate risk of local extinction without supplemental stocking (Eck and Brown 1985). Introduced salmonines that exhibit relatively higher levels of wild reproduction might persist, but over time and fluctuating ecological conditions these local populations would also face the risks of local extinction.

Some Great Lakes fisheries managers have recently adopted an unorthodox position regarding wild reproduction of introduced salmonines in the Great Lakes:

> *"Information on relative contribution of stocked and wild chinook salmon was also needed to determine the level of population control potentially available to managers through changes in stocking. There was concern by some biologists that chinook salmon and other nonnative salmonines might compete with lake trout and negatively affect lake trout restoration in Lake Superior. Management agencies on Lake Superior, under guidance of the Great Lakes Fishery Commission, documented fish community objectives for Lake Superior (Busiahn 1990). The Lake Superior fish community objective for chinook salmon and other nonnative salmonine predators was a predator–prey balance that allowed normal growth of lake trout. This objective was based on the premise that nonnative salmonine populations could be regulated by stocking. Lake trout growth decreased during the 1980s (Hansen et al. 1994), and competition with nonnative salmonines, especially chinook salmon, for decreased abundance of the major forage fish, rainbow smelt Osmerus mordax, was suspected to be a factor (Conner et al. 1993; Negus 1995). If most chinook salmon in Lake Superior are naturally produced, our ability to regulate this species to benefit lake trout would be greatly reduced."* (Marcogliese and Casselman 1998, p. 56)

It can be noted from the preceding quotation that fisheries managers are beginning to reconsider the issue of self-sustaining, wild reproduction by introduced salmonines in the Great Lakes. Perhaps this isn't such a desirable thing after all:

> *"Natural reproduction of salmonines threatens the sustainability of this community, so artificial propagation, which can be quickly curtailed if needed, is logically preferred as the source of recruitment."* (Eshenroder and Burnham-Curtis 1999, p. 174)

Human control of introduced salmonine populations through hatchery-dependence, for the ultimate benefit of native lake charr. Good grief — what a tangled web we weave.

3.1.4 Alteration of life-history characteristics

Evolutionary changes do not stop when organisms are introduced to a new ecosystem. Given the likelihood that the recipient ecosystem will differ from the native ecosystem in many varied ways, it should be expected that the introduced species will evolve away from its native state as it deals with the new conditions. These evolutionary changes can be surprisingly rapid (i.e., over the course of a few generations), and can result in the expression of variations not expressed in the native environment (e.g., Tilzey 1977; Teel et al. 2000). For example, interpopulation differences in several adult phenotypic traits suggest that chinook salmon introduced to New Zealand have been evolving into new forms — in response to novel environmental conditions encountered (Quinn and Unwin 1993; Quinn et al. 1996, 1998; Kinnison et al. 1998). This phenomenon of evolutionary change can increase the range of ecological effects that an introduced species may have on the recipient ecosystem. It becomes very difficult to predict what these changes and consequences would be, although there is probably an envelope of potential change for each species.

Human transplantation of salmonines to the Great Lakes ecosystem has put these species into a novel environment with which they had no evolutionary history. It is important to realize that when these fishes were released into the Great Lakes basin, epigenetic and genetic forces began shaping the populations — evolving new forms which, if they could survive and maintain self-sustaining reproduction, would be better adapted to persist in the new ecosystem (Alexander 1985; Krueger et al. 1994). Following this evolutionary argument, chinook salmon in Lake Huron cannot be considered to be the same ecological form as chinook salmon in British Columbia.

Even before the recent era of salmonine introductions to the Great Lakes, biologists were well aware of the 'bewildering variability' of these species when compared across different environmental conditions in their native distribution (Withler 1966; MacKay 1969; Scott and Crossman 1973). Not only did the species express a high degree of flexibility in form and function, these characteristics appeared to change rapidly after transfer to a new environment (McCart and Anderson 1967; Biette et al. 1981; Withler 1982; Li and Moyle 1993). Such variability in response to environmental conditions surely would make prediction of life-history shifts a very difficult matter (Bidgood and Berst 1967; Christie 1968; Kocik and Taylor 1987*b*).

Gharrett and Thomason (1987) reported a loss of genetic variability in Great Lakes populations of pink salmon relative to those from the source of the transplant in British Columbia. The authors argued that selection for physiologically tolerant phenotypes may have been necessary to establish the unique, self-perpetuating freshwater populations:

> *"This adaptively distinct lineage produced by the ecological change coupled with the [evolutionary] bottlenecks may be a major step toward speciation."*
> (Gharrett and Thomason 1987, p. 787)

Thus, at the level of molecular biology, there is evidence that introduced salmonines have undergone rapid evolutionary change due to the selection pressures of their new environment (see also Dueck and Danzmann 1996).

Most alterations observed in life-history characteristics of salmonines introduced to the Great Lakes were unplanned by proponents of the introductions. For example, consider the following description of how Great Lakes introductions caused considerable morphological changes in coho salmon:

> *"It is interesting to note the effect on meristics of moving a species with rather plastic characters, from different areas of its natural range, subjecting them to different embryonic development in different eastern hatcheries and liberating them into the same exotic habitat, as well as into the wide range of conditions from Lake Superior to Lake Ontario. ... Early attempts to identify salmon from the Great Lakes and to provide characters to separate exotic salmon from rainbow trout, led to confusion as a result of depending, for the salmon, on published figures of meristics of Pacific populations."* (Scott and Crossman 1973, p. 159)

Similar kinds of morphological shifts, presumably resulting from the effects of physiological, developmental or evolutionary forces in the new environment, were observed in all other species of Atlantic and Pacific salmonines. For example, Berg (1979) reported a significant shift in the morphology of both male and female pink salmon in the Great Lakes, compared to those in their native Pacific waters. Bidgood and Berst (1967) provided evidence of regional differentiation of rainbow trout meristics and morphology from various Great Lakes, suggesting that these differences may reflect differences in environmental factors between regions (e.g., water temperature, forage base).

In addition to morphological changes, introduced salmonines in the Great Lakes have also exhibited some astounding life-history shifts in their already diverse styles of reproduction. When pink salmon established new spawning runs between the typical odd-year runs, this phenomenon was recognized by biologists as a remarkable and ecologically significant change in life-history (Scott and Crossman 1973; Kwain and Chappel 1978; Gharrett and Thomason 1987):

> *"The adaptation to a presumably hostile environment coupled with the breakdown of a formerly rigid year-class structure is consistent with the notion that the pink salmon of the Great Lakes is a lineage adaptively distinct from the parent population."* (Gharrett and Thomason 1987, p. 791)

In fact, the Great Lakes pink salmon switched from their the normal 2-year cycle (odd-years) of reproduction, to 3-year-old spawning runs (Kwain and Chappel 1978; Wagner and Stauffer 1980; Nicolette 1983) as well as to precocious 1-year-old spawning runs (Kwain and Kerr 1984). There have also been reports of astounding variability in spawning migrations of rainbow trout in the Great Lakes (Biette et al. 1981). Georgian Bay rainbow trout were initially reported to spawn in their normal spring season, but investigators reported shifts to additional spawning runs in a period from autumn to winter (Dodge and MacCrimmon 1970; Dodge 1972; Dubois et al. 1989):

> *"The extended spawning season in Bothwell's Creek, characterized by two separately migrating populations, is evidence of the plasiticity of the rainbow to adapt migration and spawning patterns to local environmental conditions. Whether the basis for the distinct winter and spring spawning groups is genotypic or phenotypic has not been resolved, but the biological characteristics of the Bothwell's Creek populations merit further considerations."* (Dodge and MacCrimmon 1970, p. 617)

Chinook salmon in the Michipicoten River (Lake Superior) have been reported spawning in the spring, a phenomenon that had never been reported anywhere else in the distribution of this species (Kwain and Thomas 1984). According to Peck et al. (1999):

> *"Since the initial introduction of Green River strain in Lake Superior, mainly progeny of chinook salmon from Lake Michigan have been stocked. Minnesota introduced a spring spawning strain of chinook salmon from Idaho and Washington during 1974—1978. These fish entered Lake Superior tributaries about a month earlier than the Lake Michigan strain but otherwise held no advantage over the more easily obtainable Lake Michigan strain (Close et al. 1984)."* (p. 155)

Unwin et al. (1999) reported that chinook salmon in hatchery environments have been observed to exhibit iteroparous (multiple spawning) reproduction, in contrast to their more typical semelparous (one time) spawning behaviour. In Lake Michigan, there is also evidence that some chinook salmon may be living 5 or 6 years before spawning, in contrast to the usual 3 or 4 years before spawning and dying in the tributaries (Stewart and Ibarra 1991). In contrast, Smith (1968) reported the existence of precocious male coho salmon after the 1966 Lake Michigan stocking programs, describing their existence as an "*unusual success*." Based on this evidence, it is likely that life-history shifts observed in chinook salmon spawning runs are likely a complex result of factors both artificial (i.e., hatchery-based) and wild.

Beyond shifts in the timing of spawning runs, introduced salmonines in the Great Lakes have also demonstrated shifts in their selection of spawning habitat. Powell and Miller (1990) documented a habitat shift of chinook salmon to spawn on open-lake shoals at several locations in the North Channel of Lake Huron. Apparently, these shoal-spawning chinook salmon were also attacking and disrupting the spawning of lake charr from one of the last two wild populations in Lake Huron. Spawning in British Columbia lakes with upwellings or ground seepage is known to occur in some salmonines such as sockeye (M. Gross, personal communication, 1997) and chinook salmon (Roberson 1967; H. Regier, personal communication, 1997). Open-lake shoal-spawning has also been reported for other introduced salmonines in the Great Lakes, including kokanee (Collins 1971) and pink salmon (Kocik and Jones 1999).

Powell and Miller (1990) also observed the presence of young chinook salmon in open lake environments, suggesting that shoal spawning chinooks can use the lake as nursery habitat, rather than their normal reliance on tributaries. In contrast, Carl (1984) and Zaft (1992) reported the peculiarity of 'stream-type' chinook offspring which remain in natal tributaries of the Great Lakes through their second winter.

Not all life-history shifts exhibited by introduced salmonines in the Great Lakes are due to wild processes. As mentioned in Section 2.2.1, Great Lakes fisheries managers have tinkered with artificial hatchery production of "*superchinook*" that live longer, eat more, grow faster and grow to a much larger body size than the typical Great Lakes chinook salmon (Kitchell and Hewitt 1987; OMNR 1987). Such artificial manipulation of life-history has been recognized as significantly amplifying the ecological risks associated with this introduction:

> *"An energetics modeling analysis of sterile chinook salmon in Lake Michigan suggests certain considerations with regard to development of a trophy fishery:*

> (1) *The total impact of sterile fish on forage species is approximately 50% greater than that of the same number of standard fish stocked. A stocking program including sterile fish should take into account the higher impact and the timing of that impact in formulating policies for the total stocking program.*
>
> (2) *A cohort of sterile salmon may yield a slightly lower total return to the fishery. Certainly the yield will not increase in proportion to the high impact of sterile fish on the forage base. Given a finite resource, stocking sterile fish implies stocking fewer standard fish over each of several years, also having the effect of lowering yield. That cost must be weighed against the socioeconomic value of a new trophy fishery.*
>
> (3) *There is the possibility that large sterile salmon will prey upon other valuable species (*Coregonus *spp. and/or smaller salmonines). An unknown ecological risk exists in that the configuration of current food webs may be substantially altered by the addition of predators that attain large size during their extended life span.*
>
> (4) *Although a trophy fishery is likely to develop, the concentrations of contaminants in these large fish will probably make them unsuitable for human consumption. Agencies must accept the responsibility for informing the public of this potential hazard."* (Kitchell and Hewett 1987, p. 389)

Although it may be difficult to grasp the importance of life-history modifications, it is important to consider two essential ideas. First, introduced salmonines in the Great Lakes were already known to be creatures capable of great flexibility in form and function. Second, these fishes were introduced to an environment with environmental and community conditions very different than in their native ranges. Combining these two factors would logically predispose the introduced salmonines to change from their original state in ways which were, and still are, difficult to predict.

3.2 Effects of introduction on the Great Lakes ecosystem

A non-native organism introduced to a new environment will continue to exist only if it is able to forge a new 'niche' in the recipient ecosystem. Fisheries biologists have learned from experience that the introduction of a non-native fish into a new ecosystem cannot occur without ecological effects on the structure and function of that ecosystem (Radonski et al. 1984; Whittier and Kincaid 1999). The effects of fish introductions vary in kind, intensity and detectability — depending on the characteristics of the introduced fish species and the abiotic and biotic conditions of the recipient ecosystem (Dill and Cordone 1997). For example, spatial analyses have revealed that regions with relatively low diversity of native fish species (especially 'game' fishes) tend to have received a greater number of attempted intentional introductions, yet have typically received less ecological assessment (Nico and Fuller 1999; Rahel 2000). An FAO (1999) analysis of aquatic introductions showed that the Great Lakes drainage basin ranks among the most highly disturbed systems in North America.

I follow Kohler and Courtenay (1986), Li and Moyle (1993) and Krueger and May (1991) to categorize the ecological consequences of fish introductions as follows:

- Diseases and parasites
- Predation
- Competition
- Genetic alteration
- Environmental alteration
- Community alteration

These six categories represent a wide variety of ecological effects that have been suspected or shown to result from fish introductions throughout the world. Some of the categories (e.g., predation, environmental alteration) represent the effects of direct ecological interaction, while all of the categories represent processes which may indirectly affect the abiotic and biotic conditions of the recipient ecosystem via cascading consequences of the introduction (Kohler and Courtenay 1986; Moyle et al. 1986). It should be noted that in the following subsections, I have focussed predominantly on the ecological effects of the introduced fishes on native members of the recipient ecosystem, rather than on other non-native species which may have invaded or been intentionally introduced.

One final note is warranted before proceeding to examine evidence for effects of introduced salmonines on the Great Lakes ecosystem. In their review of Pacific salmonines in the Great Lakes, Kocik and Jones (1999) present a section entitled '*Effects of Pacific salmonines on native species*' which leads with this preamble:

> *"An examination of the potential effects of Pacific salmonines on Great Lakes native fishes requires an appropriate context. Pacific salmonines have been present in the Great Lakes for over one hundred years. During this time the physical environment and the biological communities of all of the Great Lakes have undergone profound changes. Within the lakes themselves, invading species such as sea lamprey and alewife have contributed to a fundamental alteration of fish community structure. In the watershed, dam construction, land development (urbanization, agriculture, forestry), and water uses (withdrawls [sic] and discharges) have greatly altered the physical habitats of innumerable tributaries, thereby affecting access to and suitability of these systems for fishes. Many of these changes are not reversible due to the current priorities of society, so returning the Great Lakes basin to an historic state is not a practical management objective. Nevertheless, management agencies continue to view the conservation and restoration of native species a priority (OMNR 1992). It is important, therefore, to consider whether Pacific salmonines - naturalized or hatchery-derived - are likely to affect native species populations and to judge whether these effects are significant relative to the myriad of other factors that might affects these populations."* (Kocik and Jones 1999, p. 474)

While I may disagree with the authors about ecological dynamics and public opinion, I agree with their caution about the ecological effect of introduced salmonines relative to the host of other (typically anthropogenic) stresses involved.

3.2.1 Diseases and parasites

The practice of obtaining fish from one location and introducing them to a new ecosystem inherently carries the risk of introducing and transferring pathogens and parasites, especially to native fish species in the recipient ecosystem (McDowall 1978; Hoffman and Schubert 1984; Shotts and Gratzek 1984). Viruses, bacteria and parasites typically exist on or in fish at all developmental states (i.e., eggs, embryos, juveniles, adults). Once the introduced fish and its associated organisms have been released to the wild, there is the possibility that the pathogens and parasites may find new hosts in the recipient ecosystem. When this occurs, the disease and parasitic effects can decrease survival of the new hosts (Li and Moyle 1993). The process of transferring diseases and parasites with introduced salmonines has been widespread (e.g., Roberts and Shepherd 1974; Poff 1997), and some pathogens and parasites have caused very high mortalities in native salmonine populations (Tilzey 1977).

The documentation of disease and parasite introductions to the Great Lakes, facilitated by the introduced salmonines, has generally been poor (Krueger and May 1991, P.T.K. Woo, personal communication, 1997). In the late 18th and early 19th centuries, no safeguards were apparently taken to monitor or prevent the transfer of bacteria, viruses and invertebrate parasites. As a result, it is difficult to determine whether a particular pathogen or parasite is native to the Great Lakes, or whether it was introduced. Notwithstanding this caveat, it has become abundantly clear in recent years that disease epidemics in American (federal and state) and Canadian hatcheries have plagued the introduced salmonine stocking programs (Keller et al. 1989; Brown et al. 1999). The question remains: what effect has the artificial culture and transmission of these hatchery diseases had on native species in the Great Lakes ecosystem?

Currently, we can be reasonably confident that furunculosis and whirling disease were introduced to the Great Lakes ecosystem via the release of non-native salmonines to the wild. Furunculosis is a disease condition associated with the formation of furuncles, boil-like lesions, in various tissues of the body (Post 1987). This condition is caused by a bacterium, *Aeromonas salmonicida*, that was suspected to have been introduced to the Great Lakes with the release of brown trout from Europe before 1902 (McCraw 1952; Mansell 1966; but see Duff and Stewart 1933). Ulcerative disease and erythrodermatitis have also been caused by this bacterium (Bullock et al. 1983). Furunculosis is considered to be a scourge of native salmonids (including Atlantic salmon, brook charr, lake charr, grayling and lake whitefish) which also serve as primary hosts to numerous nonsalmonid species such as dace, minnows, catfish, sticklebacks, northern pike, sculpins and yellow perch (McFadden 1970; Post 1987). Ironically, introduced salmonines such as rainbow trout are apparently less susceptible to furunculosis than are native salmonines such as brook charr (Cipriano and Heartwell 1986). Although furunculosis release into the Great Lakes is rarely documented, Behmer et al. (1993) did describe a situation where Atlantic salmon with signs of furunculosis were intentionally released into the St. Marys River.

Whirling disease is a condition caused by a parasitic protozoan, *Myxobolus cerebralis* which spends part of its life-cycle in *Tubifex tubifex*, an oligochaete worm (Mills et al. 1993). This species of *Myxobolus* is thought to have originated in central Europe and was probably introduced to North America along with back-transfers of rainbow trout prior to 1956 (Hoffman et al. 1962; Hoffman and Schubert 1984; Marnell 1986). The disease was first observed in the Great Lakes basin in 1968 at a private aquaculture facility in Ohio (Mills et al. 1993). The name 'whirling disease' was coined to describe the peculiar swimming activity of fishes infected with the protozoan; the organism causes the distortion of cartilage and bone tissue, altering the inner ear control of the fish's balance (O'Grodnick 1979; Wolf and Markiw 1985; Post 1987). The condition is also called 'black tail disease' when it occurs in juvenile salmonids, in reference to lesions produced by the parasite when it attacks the innervation tissue controlling pigmentation in the tail region. As with furunculosis, all native and introduced salmonids are susceptible (Yoder 1972); it is also possible that birds and aquatic mammals are involved in the transmission cycle (Taylor and Lott 1978). According to Kocik and Jones (1999) a whirling disease outbreak in 1994 forced the destruction of an entire year's production of steelhead for Lake Ontario sport fisheries.

Two other disorders, bacterial kidney disease (BKD) and infectious pancreatic necrosis (IPN), are also closely associated with introduced salmonines in the Great Lakes. While it is suspected that one or both of these diseases were introduced along with non-native salmonines (e.g., O'Hanlon 1982), the lack of historical records makes it impossible to prove.

Although some fisheries researchers are reluctant to hypothesize about transmission pathways between introduced and native fishes in the Great Lakes, there is evidence that *Renibacterium salmoninarum* — the pathogen that causes BKD — is transmitted among both introduced and native salmonines (Mitchum et al. 1979). BKD has been associated with severe chinook salmon mortalities in Lake Michigan (Nelson and Hnath 1990; Kabré 1993; Mesa et al. 2000):

> *"At least two hypotheses were initially proposed to explain the outbreaks of BKD and the salmon die- offs: (1) stress from depletion of alewives; and (2) a more virulent disease organism or lower resistance to the disease organism because of salmon propagation in hatcheries (R. Rybicki, Michigan Department of Natural Resources, personal communication). Evidence was also found of a genetic component in resistance of coho salmon to the bacterium (Withler and Evelyn 1990)."* (Brown et al. 1999, p. 364)

Prior to 1997, *R. salmoninarum* had been documented only among the Great Lakes salmonines proper (including transmission to lake charr despite modern disease control measures). However, recent surveys in Lakes Michigan and Huron have detected the bacterium for the first time in other fishes, including two important native coregonines — lake whitefish and bloater (LHMU 1998; Jonas et al. 1999). Fisheries managers on Lakes Huron and Ontario have expressed concern that they may face a repeat of the Lake Michigan BKD outbreak if the introduced salmonine stocking programs continue to exceed their lake's carrying capacity (LHMU 1998; Rand and Stewart 1998b). Pathologists on the Great Lakes Fish Disease Control Committee reported that 100% of the lake charr sampled from Lake Michigan tested positive for BKD, yet risks to native species (e.g., lake charr) have apparently been discounted by Great Lakes fisheries managers in response to pressure from the sport fishery to maximize stocking programs (Eshenroder et al. 1995).

Parasites, both introduced and native to the Great Lakes drainage basin, are also transmitted from introduced salmonines to native members of the Great Lakes ecosystem. Hnath (1969) hypothesized about parasite transfer between coho salmon and lake charr, in particular the acanthocephalan worm *Echinorhynchus salmonis* moving via a crustacean intermediate host, or by ingestion of prey fish tissue. Nicolette and Spangler (1986) reported that 97% of pink salmon on spawning migrations in Lake Superior tributaries were found to have the parasite *Echinorhynchidae* in their small intestines. Alewife, which are currently a dominant prey species of both lake charr and introduced salmonines, is known to be an important intermediate transport host for several helminth species.

A survey of the reported parasites of Pacific salmonines in the Great Lakes (Muzzall 1995*a*), reveals the occurrence of at least two parasites that are native to the Pacific coast of North America, and which may have been introduced through salmonine stocking programs: the nematode *Philonema oncorhynchi* and the crustacean *Ergasilus nerkae* (B. Ardelli, University of Guelph, personal communication, 1997). Muzzall (1995*a*, *b*) reports that a minimum of 22 parasites have been found in common between lake charr and Pacific salmonines of the Great Lakes (Table 4). Some of these parasites of lake charr may cause reduced growth, reduced survival, reduced swimming performance, ulcerous lesions in swim bladders, intestinal haemorrhage and inflammation that reduces nutrient uptake (Muzzall 1995*b*).

The introduction and spread of diseases and parasites to native fishes of the Great Lakes is beginning to receive more attention by aquatic biologists and fisheries managers. Recently, expanded effort has been put into the development of disease control programs among management agencies to reduce the risk of introducing new diseases and the further spread of those already introduced to the Great Lakes (Meyer et al. 1983; Horner and Eshenroder 1993; Hnath 1993).

Finally, it should be noted that the introduction of highly mobile salmonines has been associated with increased abundance and dispersion of native parasites on native fish species in the Great Lakes community, especially the acanthocephalan *Echinorhynchus salmonis* and the nematode *Cystidicola farionis* (Muzzall 1995*a*). In this case, the introduced salmonines act as a vector or intermediate host of parasites on native species; a transfer mechanism which is largely independent of charr abundance and which loads the native species with artificially elevated levels of parasites. Krueger and Spangler (1981) warned against planting fish species with migratory habits (e.g., introduced salmonines) in the Great Lakes to prevent the passive transport of adult sea lamprey out of their home population areas.

3.2.2 Predation

The introduction of a predator into a system that contains prey species which are not evolved to counter their specific predation style can lead to ecologically significant changes in the abundance and diversity of prey (Zaret and Paine 1973; Li et al. 1987; Arthington 1991; Holik 1991). Many introduced fishes are "generalist vertebrate predators," and as such they often demonstrate a remarkable ability to switch prey in a dramatic and unpredictable manner, leading in some cases to the local decimation or even extinction of native prey populations (Kohler and Courtenay 1986). In the case of introduced salmonines, predation is typically documented only during the adult and perhaps juvenile periods of development, without regard to the ecological effect of different prey selections earlier in life-history (Taylor et al. 1984).

There are numerous, worldwide examples for the profound ecological effect of predation by introduced fishes, especially salmonines. McDowall (1968, 1978)

Table 4. A list of parasites reported in common for lake charr (*Salvelinus namaycush*) and introduced Pacific salmonines (*Oncorhynchus* spp.) of the Great Lakes. Sources: Muzzall (1995*a*, *b*).

Class/Order	Species
Cestoidea	*Cyathocephalus truncatus*
	Diphyllobothrium sp.
	Eubothrium crassum
	Eubothrium salvelini
	Proteocephalus parallacticus
	Triaenophorus crassus
	Triaenophorus nodulosus
Nematoda	*Capillaria salvelini*
	Cystidicola farionis
	Cystidicola stigmatura
	Rhabdochona sp.
	Spinitectus sp.
Acanthocephala	*Acanthocephalus dirus*
	Echinorhynchus lateralis
	Echinorhynchus leidyi
	Echinorhynchus salmonis
	Noechinorhynchus tumidus
	Pomphorhynchus bulbocolli
Crustacea	*Ergasilus caeruleus*
	Ergasilus luciopercarum
	Ergasilus nerkae
Fungi	*Saprolegnia* sp.

described the evolutionary reasons for the high susceptibility of native freshwater fauna in New Zealand waters to predation by introduced rainbow trout. Jackson (1975) and Tilzey (1976) both concluded that native galaxiid fishes in New Zealand were unable to withstand introduced trout predation, leading to the local extirpation of certain species.

The most frequently cited example of predation effects by intentionally-introduced fishes in North America is the widespread decline in populations of native salmonines associated with attempted introductions of European brown trout (e.g., Moyle 1976*a*, *b*; Alexander 1979). However, reasons for the decline of the native salmonines are often intertwined with other anthropogenic stresses (e.g., dam construction, logging, urbanization).

Although most studies in the Great Lakes have focussed on the diet of adult salmonines, the reader must consider that these organisms feed at all post-embryonic life-history states during development. Whether an individual fish is released from a hatchery or produced via wild reproduction, it must still obtain energy from the ecosystem for the time that it is in the wild:

> *"The problem is less manageable as regards trophic levels, at least in regard to fish. The problem here is that with fish (to a greater extent than with most birds and mammals) an individual organism in its history usually passes through a series of trophic levels, i.e., from herbivore or primary predator, to secondary predator and with age perhaps to tertiary or higher levels. This fact is overlooked surprisingly frequently by fishery biologists. It has basic relevance to the question of which species to introduce; it has in fact been taken into account in some recent proposals (e.g., Maher, 1964; Tody and Tanner, 1966)."* (Regier 1968, p. 97)

Unfortunately, we have relatively little quantitative information about the predatory habits of introduced salmonines in the Great Lakes. For example, Stewart and Ibarra (1991) did not attempt to evaluate predation by wild-spawned, introduced salmonines in Lake Michigan — one of the best studied of all Great Lakes — simply because of insufficient data. There is evidence to show that diets of open-lake, adult salmonines have been typically dominated by alewife and rainbow smelt (see below); however, closer examination of the literature shows that introduced salmonines are not the specialist alewife/smelt biological control agents that many people believe.

The unplanned predation on native species by introduced salmonines can have substantial effects on the prey populations, especially when stocking programs exceed local carrying capacity. Brandt (1986) noted that while the occurrence of some native prey species in Lake Ontario salmon diets was low relative to leading components (i.e., non-native alewife), the predation rate may be ecologically significant to the native prey populations. Very few of these native species are considered to be economically important.

For the purposes of this review, I have distinguished between salmonine predation effects by introduced salmonines at two developmental states (juveniles and adults), and in two qualitatively different environments within the Great Lakes basin (tributaries and lakes).

Juvenile introduced salmonines

Tributaries

Depending on the species of introduced salmonine, juveniles may spend from one to several years in a natal tributary (Scott and Crossman 1973; Biette et al. 1981). During this time, juveniles commonly forage on benthic invertebrates, including those originating from either the aquatic or terrestrial environments (MacKay 1969; Johnson and Ringler 1979*a*).

Coho salmon juveniles generally feed on insects, with a preference for immature stages. The preferred food of yearling coho salmon from Lake Michigan tributaries includes mayflies, water boatmen and Dipterans, with stoneflies and beetles being of lesser importance (Peck 1974). Wagner (1975) found that coho salmon from the Platte River (Lake Michigan) fed largely on caddisflies, blackflies, mayflies and homopterans (see also OMNR 1988). Johnson (1978), Johnson and Ringler (1981) and Johnson (1981) found that recently emerged coho salmon in a Lake Ontario tributary fed extensively on a wide variety of terrestrial and aquatic invertebrates, including chironomid larvae and pupae, homopterans and ephemeropteran naiads. The authors suggested that the availability of food for post-emergent individuals may be an important consideration in determining the carrying capacity of these streams for both native and non-native salmonines.

All of the juvenile chinook salmon examined by Johnson (1981) in a Lake Ontario tributary contained food with the principal prey being fish eggs, adult chironomids and terrestrial coleopterans in 1980, and adult chironomids and homopterans in 1981. Although the fish eggs could not be identified, the salmon collected in 1981 were associated with large numbers of emerald shiners from which ripe eggs and milt were easily extruded, making them a likely candidate.

Juvenile rainbow trout examined by Kwain (1983) from Stokely Creek (Lake Superior) generally foraged on the organisms that were available (e.g., larvae and adults of Coleoptera, Hymenoptera, Lepidoptera, Hemiptera, Homoptera and Diptera). He reported that smaller rainbow trout (<7 cm) fed more on benthic organisms than terrestrial insects, while larger fish (>14 cm) consumed more terrestrial insects than benthos. Johnson and Ringler (1979*a*) reported that rainbow trout juveniles in a Lake Ontario tributary fed on a wide variety of terrestrial and aquatic invertebrates.

Lakes

Kocik and Jones (1999) commented that very little information has been collected on the foraging habits of juvenile introduced salmonines in open lake environments of the Great Lakes. Nearshore zones of the Great Lakes are considered important nursery areas for many juvenile salmonines except lake charr, which typically inhabit very deep waters (Jude et al. 1987). Juvenile introduced salmonines in Lake Michigan have been collected in relatively warm (>20°C) beach-zone waters where they were feeding on terrestrial insects concentrated at the surface (Jude et al. 1987). English (1983) and Kwain (1983) both found that juvenile rainbow trout and chinook salmon consumed floating insect prey. It should be noted that juvenile introduced salmonines may also forage on alewife; growth of brown trout and coho salmon during their first year in Lake Ontario was positively correlated with numerical abundance of young alewife (O'Gorman et al. 1987).

Post-smolt coho salmon observed by Peck (1974) in an estuary and bay on northern Lake Michigan fed primarily on nymphs and larvae of aquatic insects (e.g., mayflies, water boatmen, dipterans, stoneflies and beetles). These juvenile coho salmon also consumed crustaceans, amphipods, isopods, copepods, cladocerans and oligochaetes.

During their first summer in the lake, chinook salmon seem to feed in an opportunistic manner, largely on terrestrial insects taken at the surface in nearshore waters (Stewart et al. 1981; OMNR 1988). Diet studies of age-0 chinook salmon in nearshore Lake Michigan habitats indicated that they fed primarily on terrestrial insects, larval fish, larval aquatic insects and zooplankton; by late summer their diet had already shifted to small fishes (Elliott 1994).

Jude et al. (1987) reported that stomachs of small, nearshore rainbow trout had the highest proportion of invertebrates (17–100% over all three seasons) found in any of the Lake Michigan salmonines.

Adult introduced salmonines

Tributaries

Bowlby and Roff (1986) surveyed several small Great Lakes tributaries in southern Ontario and found predation by fishes — notably the introduced salmonines — to have more of an influence on diversity and abundance of invertebrates than did energy availability in the ecosystem. Effects of predation by introduced salmonines in such tributaries will be severe in situations of low productivity and in cases where stocking has resulted in very high densities of these predators. Ellis and Gowing (1957) and Stauffer (1977) determined that trout growth was indeed limited by food in the less productive sections of Michigan streams. Stauffer (1979) presented evidence that elevated numbers of introduced salmonine offspring may have depleted food resources in Lake Superior tributaries. As stream-resident introduced salmonines grow larger, there is a transition from preying on invertebrates to vertebrates, particularly other fishes (MacKay 1969; Scott and Crossman 1973).

Diet studies have shown that brown trout tend to shift their primary food source from insects to fish at about the same size (i.e., 350–400 mm) at which Shetter (1968) and Jenkins (1969) observed increased levels of instream movement. Shetter and Alexander (1970) provided evidence that brown trout in a Lake Huron tributary had a high proportion of small trout in their diet.

Johnson (1981) reported that adult brown trout fed primarily on decapods, frogs and juvenile coho salmon and rainbow trout in the Salmon River (Lake Ontario). Stauffer (1977) found that stomachs of 76–152 mm brown trout from the Au Sable River (Lake Huron) contained 100% invertebrates, whereas stomachs of 152–254 mm brown trout contained 93% invertebrates and 7% fish by weight. Brown trout are known to be intense piscivores in streams, with a reputation for feeding extensively on native brook charr (Alexander 1977) and on young of their own species (Idyll 1942; MacKay 1969). In the Au Sable River, Alexander (1977) reported that the diet of brown trout larger than 305 mm was composed of 25% invertebrates and 75% fish by weight. Evidently, brown trout smaller than 400 mm tend to be stationary drift feeders (Clapp et al. 1990). Alexander (1977) found that adult brown trout consumed 4,728 and 2,219 age-0 brook charr per stream kilometre in two sections of the river, while eating only 135 juvenile brown trout in the same waters.

Johnson (1981) found that adult rainbow trout in the Salmon River watershed (Lake Ontario) consumed mostly terrestrial annelids, trichopterans, semi-aquatic vertebrates and decapods. Christie (1973) reported that stream-resident rainbow trout preyed on kokanee juveniles that had been stocked in Lake Ontario tributaries. Stream-resident rainbow trout have been experimentally shown to significantly reduce stonefly abundance in a Lake Ontario tributary (Feltmate and Williams 1989); of the observed 35% decline in stonefly density, some of that decline was attributed to the direct effects of predation but more loss was due to emigration of stoneflies from the predator-stressed section of the stream. Feltmate and Williams (1989) considered this level of predator effect to be a significant threat to the survival and growth of stoneflies in the wild.

Spawning migrations in tributaries

It is important to consider that native communities in Great Lakes tributaries evolved without the presence of numerous, large piscivorous fish that made spawning runs in either the spring or autumn (MacCrimmon 1977; but see Loftus 1958 for a description of river-spawning lake charr). Some authors have indicated that adult, introduced salmonines have been known to kill, if not consume, native fish during spawning runs — especially smaller species and juvenile fishes using the tributaries as a nursery ground (Alexander 1977, 1979; Fausch and White 1986).

Hildebrand (1971) provided evidence indicating that, while coho and chinook salmon may aggressively strike smaller organisms during spawning runs in the river, they do not forage at levels characteristic of the open-lake environment. Fewer than 15% of pink salmon on spawning migrations in Lake Superior tributaries had food in their stomachs, and this was mostly food ingested in the open-lake environment (Kwain and Lawrie 1981; Kwain 1982; Nicolette and Spangler 1986).

Lakes

Most of the open-lake salmonines introduced during the recent era have survived quite well in all of the Great Lakes, except at times (e.g., recently) or locations (e.g., Lakes Superior and Erie) where alewife were relatively scarce (Jude and Leach 1993). In fact, there is substantial evidence indicating that both alewife and rainbow smelt have been major prey items in the diet of open-lake, introduced salmonines (Stewart et al. 1981; Brandt 1986; Jude et al. 1987; Rand and Stewart 1998*a*, Harvey and Kitchell 2000).

Jude and Leach (1993) suggested that the dominance of alewife in the diet of introduced salmonines may be associated with two factors: (1) the possibility that alewife are more pelagic, slower swimming and densely schooling compared to native prey species, and (2) the observed propensity of introduced salmonines to feed at mid-water depths.

Differences among introduced salmonines in alewife predation

It should be noted that not all introduced salmonines in the Great Lakes are equally capable of preying upon alewife and rainbow smelt. Rainbow trout are perhaps the least capable of the salmonines, catching alewife in pelagic waters only when reactive distances are small. In contrast, pelagic alewife are easily captured by chinook salmon, which often ignore yellow perch (J. Savitz, personal communication cited in Jude et al. 1987). It is no surprise that chinook salmon consume the greatest proportion of alewife production compared to other stocked salmonines (Stewart et al. 1981; Brandt et al. 1991). Jude et al. (1987) believed that alewife are more vulnerable prey to effective pelagic predators, relative to native species such as bloater. These authors argued that alewife have not fully adapted to life in freshwater, as exemplified by their iodine deficiencies (Colby 1973), and by mass mortalities in cold winters (Eck and Brown 1985).

Effect of introduced salmonine predation on alewife

From the beginning of the modern stocking programs, the possibility that introduced salmonines could eat up their forage base was recognized (Carter 1968).

Stewart et al. (1981) warned of the danger of overstocking salmonine predators that consume alewife and other prey in Lake Michigan at rates more proportional to their own densities, rather than the density of prey; e.g., they are efficient predators and consume what they need even at low prey densities (Negus 1995). A rapid switch to other prey species could depress those populations before any management action based on stocking rates could be effective (Stewart et al. 1981). Indeed, alewife abundance has declined in Lakes Michigan and Ontario after intensive stocking of the introduced salmonines (Jude and Tesar 1985; Eck and Wells 1987; Evans 1990; Jones et al. 1992).

There are a host of indirect ecological effects that could stem from a decline in alewife that was caused by predation of introduced salmonines:

> *"It seems safe to assume, however, that in recent years [introduced salmonines in Lake Michigan] may have affected the abundance of alewives, their main item of diet, and in doing so may have affected some native species that have important interrelations with the alewife."* (Wells and McLain 1972, p. 893)

Most notable among these indirectly affected species would be the lake charr, which also rely heavily (but not exclusively) on alewife and rainbow smelt as prey (Eck and Brown 1985; Jude et al. 1987; Brandt 1986; Stewart and Ibarra 1991; Miller and Holey 1992). For example, in 1979 it was estimated that alewife comprised 71% of lake charr diets in Lake Michigan (Eck and Brown 1985) and that similar estimates were made for coho and chinook salmon diets (Stewart et al. 1981).

Other caues of alewife declines

Some researchers have suggested that declines in alewife abundance are a direct result of salmonine predation (Samples and Bishop 1982; Kitchell and Crowder 1986; Hanson 1987; Kitchell and Hewitt 1987; Scavia et al. 1987). Stewart et al. (1981) argued that increasing numbers of stocked salmon in Lake Michigan 'overgrazed' the available alewife populations. However, alewife may also be profoundly affected by (1) inclement abiotic conditions, and (2) reduction of available planktonic forage in the Great Lakes. Kitchell (1985) presented correlation analyses of alewife and weather conditions in Lake Michigan during the later 1970s, suggesting that predation by salmonines was more important that weather-related effects in this case. Eck and Brown (1985) and Jude and Tesar (1985) argued that a series of extremely cold winters could have been a major factor in reducing Lake Michigan alewife abundance in 1983 to levels lower than those observed since the original invasion of this species to the lake (Eck and Brown 1985; Jude and Tesar 1985). It is also possible that the effective reduction of plankton in the Great Lakes — for example, through reduction of nutrients in human runoff/sewage, or through the action of zebra mussel filtration — could have resulted in food limitation for planktivores such as the alewife and rainbow smelt.

Prey switching by introduced salmonines

To date, most introduced salmonines in the open Great Lakes have proven themselves to be somewhat selective in their predation on alewife and rainbow smelt. According to Sprules et al. (1991), alewife and smelt make up 80–90% of salmonid diets in Lake Michigan, even though they comprise less than 30% of estimated planktivore biomass. In contrast, Lake Michigan bloater were estimated to comprise less than 20% of the introduced salmonine diets, despite the fact that they made up more than 70% of the estimated planktivore biomass. Simulations of chinook salmon feeding have suggested that their growth and survival would decline if they were forced to switch to bloater (Stewart and Ibarra 1991).

There is evidence that introduced salmonines have indeed become food limited, as suggested by the reduction in mean weights of coho and chinook salmon (Stewart et al. 1981), a downward trend in percent muscle lipid concentration (Wisconsin Department of Natural Resources unpublished data, cited by Miller and Holey 1992; LHMU 1998) and reductions in the trophy size of chinook salmon harvested by recreational anglers (Hansen et al. 1990). Stewart and Ibarra (1991) suggested that lower angler catch rates of Lake Michigan chinook salmon might reflect a change of foraging behaviour by the salmon as they seek prey other than alewife.

Some evidence suggests that Lake Michigan introduced salmonines have not yet exhibited a widespread switch from declining alewife populations to increasing bloater populations, or other native species (Hanson 1987). Jude et al. (1987) looked for evidence of prey switching by introduced salmonines in Lake Michigan; bloaters made up increasing proportions of introduced salmonine diets in Lake Michigan, especially in the autumn, but still not to a degree reflecting bloater abundance in the lake (Jude et al. 1987). Despite an 86% decline in alewife abundance, a 10-fold increase in bloater abundance and a 5-fold increase in yellow perch abundance, no diet shift had apparently occurred. Similar results were reported for Lake Ontario, but with a bit more detail on diet composition:

> *"It appears that predatory salmonines exploit fish populations much like humans do. They first harvest the easiest and most profitable resources (i.e., adult alewife) and, when harvest efficiency declines, increasingly switch to less profitable sources of energy (i.e., rainbow smelt, juvenile alewife). As was found in Lake Michigan, however, salmon did not readily switch to other abundant prey fish, like bloater. The rate of exploitation in Lake Ontario may cause further reductions in both adult alewife and rainbow smelt abundance, which may ultimately translate into reduced growth and survival among salmonines."* (Rand and Stewart 1998*a*, p. 316)

In this case, introduced salmonines were apparently working their way down the exploitation efficiency ladder — however, it was not clear how far down that ladder they had actually dropped. Although no hard evidence has apparently been collected for Lake Huron, the fisheries agencies regard bloater as being among the "most common prey species for large top predator salmonids" (LHMU 1998). Unfortunately, when it comes right down to it, we actually know very little about the extent to which introduced salmonines in the Great Lakes alter their diets (trade-offs, switches) in response to variations in prey abundance (Rand and Stewart 1998*a*).

Miller and Holey (1992) suggested that thermal segregation of bloater and introduced salmonines, combined with a strong preference of coho salmon and chinook salmon for tightly schooling mid-water alewife, may preclude switching to other prey species unless alewife numbers become even more limited. Jude et al. (1987) suggested that introduced salmonines were eating prey in proportion to abundance only when preferred temperatures of predator and prey overlapped; reinforcing the idea that alewife and rainbow smelt might 'buffer' other forage species from salmonine predation (Rybicki and Clapp 1966). Some researchers believe that salmon may have more difficulty catching bloater, because bloaters attain a larger size than alewife and generally inhabit deeper waters where low light levels might restrict the salmon's ability to find prey (but see below for evidence of substantial foraging on bloater) — in contrast to the more successful foraging capabilities of lake charr for bloater (Stewart and Ibarra 1991; Harvey and Kitchell 2000; O'Gorman and Stewart 1999). Elliott (1993) found that pelagic bloater juveniles were commonly found in chinook salmon stomachs, however adult bloater were rarely preyed upon. According to Martinez and Bergersen (1989), Pacific salmonines are not very successful predators on *Mysis* introduced in other North American lakes; the absence of predator–prey co-evolution, and the salmonine's dependence on sight feeding, may prevent the predator from efficiently locating the prey in deep water or at night (Eshenroder et al. 1995).

Formation of a prey search image, as Ware (1971) suggested for rainbow trout, may be delayed; perhaps explaining why salmonines still prey heavily on alewife despite increased abundance of bloaters (Jude et al. 1987). Ironically, the same kind of persistence in preying upon declining alewife and smelt has been observed in native lake charr:

> "*Although bloaters and other ciscoes were a mainstay in the diet of native lake trout before the invasion of the sea lamprey, planted trout were slow to switch from a diet of the exotic species [alewife and rainbow smelt] in Lake Michigan in the 1980's (J. Kitchell, pers. comm.).*" (Brown et al. 1987, p. 376)

It is possible that some other factor associated with planktivore predation maintains higher prey selectivity than would be expected on the basis of lakewide productivity.

Introduced salmonine predation on native species

Whether through established predator–prey relationships, or as a result of prey switching, there is evidence that introduced salmonines prey on native species in the open-lake environments of the Great Lakes. Although there may be significant political resistance to this fact in some jurisdictions, other fisheries management agencies have been more straightforward about the role of native fishes as prey for their hatchery-based introduced salmonines. For example, consider the Michigan perspective on the important role of bloater and sculpins as prey for the introduced salmon salmonines, as well as the threat perceived by non-recreational harvests of the forage base:

> "*Management of the forage base Although the future success of the salmon and trout sport fisheries depends on the proper management of a diverse forage base, management agencies have not allocated these forage species as the principal food source of the salmonid populations. Some states allow alewives, bloaters, and smelt to be harvested commercially for a low price per pound and used as pet food. Since diet studies indicate that the 311 million pound biomass of adult chubs (over 150 mm in total length) is essentially unavailable as forage, the consumption rate of available forage is approximately 28% (146 million pounds eaten out of 500 million pounds available). Although the most recent diet studies indicate a continued reliance by the major salmonine predators on alewives, salmonids will prey, to some degree, on the available stocks of bloaters and other forage species besides alewife. There are concerns about the instability of the alewife stocks and whether the predators will survive and grow*

> *as well if dependent on the other prey species (principally chubs). It would be prudent to manage for a well-balanced forage base to ensure a stable, high-density salmonid population. Alewives, bloaters, smelt, and sculpins should be managed for the purpose of securing an essential, diverse mix of forage. Therefore, a reduction or, more likely, termination of commercial operations competing for these species is inherent to the success of this management proposal.*" (Keller et al. 1989, p. 7)

It should be clear from this statement that at least some of the American Great Lakes fisheries management agencies were quite open in their desire and expectation for predation of introduced salmonines on native species such as bloater and sculpins. Any harvesting activity that might interfere with feeding of their salmon and trout should be terminated — including harvest of non-native alewife/smelt (how ironic) and the traditional commercial fisheries for bloater.

Brandt (1986) found that diets of Lake Ontario coho salmon, brown trout and lake charr were more diverse in spring than at other times of the year. Since these species often occur in nearshore waters during spring warming and prior to the alewife spawning migrations (e.g., Haynes 1983), alewife may not be as readily available during spring as they are later in the year (Wyman and Dischel 1984). On numerous occasions, researchers have indicated the high probability of predation by introduced salmonines on juvenile lake charr (Elrod et al. 1993; Elrod and Schneider 1992); however, investigation of this controversial possibility has apparently not been undertaken. Rand and Stewart (1998*a*) reported the stomach contents of the 5 major sport-harvest Lake Ontario salmonines; the native prey species included slimy sculpin, yellow perch, threespine stickleback and johnny darter. In these Lake Ontario samples, chinook salmon exhibited the least prey diversity (minimum 60% alewife), chinook salmon and rainbow trout were consistent in their preference for alewife, while brown trout (spring preference only) and coho salmon (summer preference only) exhibited seasonal trends in preference; lake charr were variable in diet preference, however they appeared to be heavily dependent (i.e., >50%) on juvenile alewife (Rand and Stewart 1998*a*).

Jude et al. (1987) presented evidence of introduced salmonine predation in Lake Michigan on other native fishes such as bluegill sunfish, johnny darter, spottail shiner, bloater and trout-perch. Negus (1995) observed that the combined introduced salmonines in Lake Superior prey on coregonines (lake herring, bloater, kiyi), insects (primarily terrestrial), crustaceans (primarily opossum shrimp *Mysis relicta*) and other small salmonines. Introduced salmonines in Lake Superior are known to rely on lake herring as an important part of their diet (Hansen 1994; Brown et al. 1999). Harvey and Kitchell (2000) noted that introduced salmonines in Lake Superior also rely upon invertebrates which have been identified as important food sources for juvenile lake charr and burbot (Hansen et al. 1995; S. Schram Wisconsin DNR unpublished data cited in Harvey and Kitchell 2000).

Brown trout have been reported to prey upon yellow perch and bloater (Jude et al. 1987) and on insects, crayfish, yellow perch, slimy sculpin and johnny darters in Lake Ontario (Brandt 1986). Rand and Stewart (1998*a*) reported that brown trout and lake charr were the only two sport-caught salmonines in their Lake Ontario samples to feed consistently on prey other than alewife and rainbow smelt (mostly slimy sculpin and yellow perch).

Coho salmon in Lake Erie have reportedly switched from rainbow smelt to yellow perch when rainbow smelt declined and yellow perch formed a strong year-class (A. Timmerman, Lake Erie Fisheries Assessment Unit cited in Jude et al. 1987). Yellow perch are readily eaten by introduced salmonines during spring or during upwellings in summer — when the nearshore waters occupied by yellow perch are cold enough to be occupied by the salmonines. (NFC-GL, unpublished data in Eck and Wells 1987). Coho salmon in Lake Superior eat *Mysis relicta*, insects, crustaceans and ninespine sticklebacks (McKnight and Serns 1974); in Lake Michigan they eat ninespine sticklebacks and insects; in Lake Erie they have been reported to feed extensively on emerald shiners (Hartman 1972; Leach and Nepszy 1976) and in Lake Ontario they eat slimy sculpins and insects in the spring (Brandt 1986). Coho salmon stocked in a Wisconsin lake preyed heavily upon invertebrates (e.g., Emididae larvae and pupae, coleopteran adults, ants, beetles, *Corixidae* larvae, cladocerans) as well as some fish and fish eggs (e.g., cisco, smallmouth bass) (Engel 1976). Engel and Magnuson (1976) found that coho salmon stocked in this inland lake exhibited spatial overlap with both yellow perch and cisco, and recommended that coho salmon not be stocked in other lakes with cisco due to the high risk of predation.

Adult chinook salmon diets have been reported to diversify in autumn and winter (when few observations are made compared to summer), perhaps due to seasonal offshore movements and recruitment of the offspring of various species to the adult chinook habitat (Stewart and Ibarra 1991). Stewart et al. (1981) presented evidence that sculpins may be an important component of chinook diets. Kitchell and Hewitt (1987) expressed concern that sterile chinook salmon may expand their diet to include lake charr, lake whitefish and other native species. Kogge (1985) and Elliott (1993) found that, in addition to feeding on alewife and rainbow smelt, chinook salmon in Lake Michigan fed extensively on bloater and yellow perch, and to lesser extents on trout-perch, sculpins, threespine sticklebacks and assorted shiners. Rybicki and Clapp (1996) examined the diets of chinook salmon in eastern Lake Michigan for the period 1991 to 1993; they found the majority of their specimens fed primarily on a mix of alewife, bloater and rainbow smelt. Perhaps most importantly, Rybicki and Clapp (1996) presented strong evidence that three key factors can significantly affect diet composition in Great Lakes chinook salmon:

(1) *body size*: small chinook salmon consumed a higher percentage of insects and other invertebrate food items, medium sized chinook salmon consumed more bloater than small or large individuals;

(2) *water depth*: small and medium chinook salmon collected in water 45 m deep consumed more rainbow smelt and bloater, those collected in water >45 m consumed mostly alewife, large chinook salmon consumed mostly alewife in both shallow and deep water; and

(3) *seasonal and year*: variation in diet across time was most pronounced for small and medium chinook salmon, diet diversity was highest in summer and diet diversity increased from 1991 to 1993.

Peck (1996) examined the contents of chinook salmon stomachs sampled during April–October from the Lake Superior recreational fishery:

> *"Of the 178 stomachs examined, 47 (26%) contained food and 131 (74%) were empty. In stomachs with food, fish occurred in 87% and made up 99% of the diet by weight. Of the 99% by weight of fish, 53% were coregonines (20% lake herring* Coregonus artedii, *18% lake whitefish* Coregonus clupeaformis, *15% unidentified), 36% rainbow smelt, 8% yellow perch* Perca flavescens, *and 2% ninespine stickleback* Pungitius pungitius. *Invertebrates were found in about 18% of the stomachs containing food, and included insects (*Ephemeroptera, Lepidoptera, Hymenoptera*) and crustacea (*Mysis, Bythothrephes, Diporeia*)."* (Peck 1996, p. 7)

Based on this evidence, chinook salmon could be more appropriately characterized as "*generalist vertebrate predators*" — eating whatever is out there; and that means mostly native species of invertebrates and fishes, when conditions like Lake Superior exist. Clearly, this introduced salmonine is anything but a specialized biocontrol agent, focussing predominantly on nuisance non-native species such as alewife and rainbow smelt.

Rainbow trout in Lake Ontario feed on slimy sculpin, johnny darter, sticklebacks and snails; however, they depend mostly on aquatic insects during the spring and summer, and alewife in the autumn (Brandt 1986; Haynes et al. 1986). Lake Michigan rainbow trout diet is more diverse, especially with additional foraging on yellow perch and bloater (Jude et al. 1987). Individual-based models developed by Madenjian et al. (1994) predicted that the general diet composition of Lake Michigan rainbow trout would be comprised mostly of invertebrates and fishes other than alewife; terrestrial insects would comprise a substantial portion (approximately 67%) of the macroinvertebrate portion of the rainbow trout diet. In inland Michigan lakes, rainbow trout have been observed to exert selective and intense predation on daphnids (i.e., *Daphnia pulex*) (Galbraith 1967).

Kokanee have been reported to feed extensively on small insects (both aquatic and aerial), occurring in 90% of the specimens examined; their diet included several insects, especially aphids, leafhoppers, dipterans, midges, fungus gnats, leafminers; and it also included plankton: e.g., cladocerans *Holopedium*, *Polyphemus* and *Daphnia*, the copepod *Cyclops* (Collins 1971). It has been demonstrated elsewhere (e.g., Lake Tahoe) that when kokanee were released to the wild, they preyed upon three different species of zooplankters so heavily that it caused their local extinction (Morgan et al. 1978).

3.2.3 Competition

Competition occurs when two organisms require the same resource that is limited in supply, leading to an ecological shift by one or both species (Moyle and Vondracek 1985; Li and Moyle 1993). Ecological theory distinguishes between two different forms of competition (Krueger and May 1991):

> ***Exploitation competition**: Use of resources that are limiting with respect to potential demand.*
>
> ***Interference competition**: Use of a resource by a species that obstructs use of that resource by another species, regardless of supply.*

Exploitation competition typically occurs when one species uses a resource more quickly and more efficiently than the other species. This phenomenon is more difficult to detect compared to the relatively conspicuous effects of interference competition, although both processes are suspected to be important in the ecological relationship between native and introduced fishes (Li and Moyle 1993).

Competition between introduced and native species is widely suspected as a dominant ecological force, despite the fact that it is difficult to demonstrate in the wild, due to its indirect nature and the complexity of other factors in survival. Although competition is frequently cited as a major cause for displacement of native fishes by introduced fishes, much of the evidence is inferential and does not conclusively demonstrate that one or more resources is actually limiting (Tilzey 1977; Fausch 1988; Ross 1991). For example, Fausch (1998) reviewed 17 published experiments on interspecific competition between juveniles of Atlantic salmon and other fishes, and he found that very few of these studies were deigned and executed in a manner that would yield the evidence required to actually determine if interspecific competition was having a significant effect. Most studies have stopped at the level of documenting overlap between the diet of introduced and native fishes (see Taylor et al. 1984); these studies lack the substantial effort required to explicitly test the predictions of competition theory (Kohler and Courtenay 1986). As a result, this operational constraint on experimental ecology may have led to a profound underestimation of the effects of introduced fishes on native organisms (Peters 1991).

In some cases, investigators have found no evidence of competition where it was expected. Burnet (1959) reported that fluctuations in introduced salmonine abundance in a New Zealand stream had no measurable effect upon the growth rate of native eels in the same drainage basin. Flick and Webster (1975) found no changes in growth and survival of introduced brook charr when non-salmonine species were removed from a small mountain stream over a 13-year period.

In contrast, there are other studies which have demonstrated that competition with introduced fishes can be an important factor in determining the survival of native species. Tests with native and introduced salmonines in streams have shown that the introduced species may engage in interference competition through aggressive behaviour for spawning sites, feeding territories and cover (Fausch and White 1986; Fausch 1988; Li and Moyle 1993). There are virtually no studies that tested the predictions of competition between introduced fishes and native species in open-lake environments. Krueger and May (1991) suggested that competition between introduced and native fishes in lakes should be less intense than in stream environments, although this would necessarily depend on the limiting resource and the ecological characteristics of the species involved.

I have selected the brook charr and lake charr for discussion in this section, largely due to the fact that most of the available literature is focussed on them. This does not mean that competition is not significant between introduced salmonines and other native species, but rather that there is little, if any, available information about them. The reader should note that competition is not something unique to interactions between native and introduced salmonines — it has also been studied between native salmonines and other native fishes as well (e.g., Magnan and Fitzgerald 1982; Tremblay and Magnan 1991). The point here is that we need to consider the force of competition in a greater ecological context; a context in which the organisms are required to survive and reproduce.

Throughout the accounts provided below, the reader should keep one important point in mind. The resource supply–demand relationship that underlies competition between introduced salmonines and native species in the Great Lakes is profoundly affected by the stocking of hatchery-reared fish. For example, the number of native salmonines spawning in any particular tributary tends to form an equilibrium with the amount of suitable spawning habitat (Krueger and May 1991). If hatchery release rates are not intimately tied to conditions in the ecosystem, stocking programs can easily disrupt ecological feedback mechanisms, and lead to chaotic changes in processes such as competition.

Competition between introduced salmonines and brook charr

In general, there is a strong negative correlation between distribution/abundance of introduced salmonines and that of native brook charr. Stoneman and Jones (2000) surveyed 118 tributaries in southern Ontario and found that brook charr maintained a strong presence in local ecosystems only if non-native salmonine biomass was lower than $0.3\ g{\cdot}m^{-2}$.

Brown trout and brook charr exhibit similar ecological requirements for habitat and food, often leading to inter-specific competition (Metzelaar 1929; Nyman 1970; Johnson 1980). Bowlby and Roff (1986) considered brook charr, brown trout and rainbow trout in tributaries to Lakes Huron, Erie and Ontario to be ecologically similar, as evidenced by the displacement of brook charr by the other two non-native salmonines in some of the streams they studied.

> *"Brown trout need clean, cold water to satisfy their living requirements. In southern Ontario, they frequent pools or ponds fed by streams. They can adapt themselves to somewhat warmer water than tolerated by our native trout. They seem to do best in water that does not exceed 80°F. Although they hold their own in many turbulent, fast-flowing streams, they appear to show a preference for quiet, placid waters like those of their native home in England, France and Germany. However, experience has shown that practically all streams that are suitable for brooks [brook charr] are suitable for browns. This adaptation to cold water and rapidly flowing streams brings them into direct competition with our native brook trout."* (MacKay 1969, p. 85)

The fact that brown trout have a greater tolerance for warmer and more turbid waters would exaggerate any effects of competition with brook charr, which tend to retreat further into the headwaters of disturbed tributaries (Scott and Crossman 1973; Krueger and May 1991). In many Great Lakes streams where brown trout were introduced or have invaded, brook charr tend to be more abundant in headwaters, and brown trout more abundant downstream (Kocik and Taylor 1996). There is often a zone where the two species overlap, but in many cases the brown trout gradually encroach further upstream over time (Fausch and White 1981). This distributional pattern may be due to one or more of the following possibilities (Fausch and White 1981):

(1) changes in physical characteristics along the stream course.

(2) differential effects of angling, owing to greater catchability of brook charr.

(3) predation by large brown trout on small brook charr.

(4) competition between brown trout and brook charr for some limiting resource.

Waters (1983) documented a change in species composition of a forested Minnesota stream over 15 years from virtually 100% native brook charr to predominantly introduced brown trout, concluding that the change resulted from competitive superiority of the brown trout. In Lake Superior tributaries, brook charr are abundant above obstructions to rainbow trout migration, whereas below these obstacles rainbow trout are much more abundant than brook charr (Krueger and May 1991). Stream-resident rainbow trout and brook charr also have a high degree of overlap in their demand for habitat, cover and food:

> *"Although behavioral interactions favor adult brook trout over other trout under circumstances of low velocity (Cunjak and Green 1983, 1984) or cold temperature (Cunjak and Green 1986; De Staso and Rahel 1994), reductions in both the range and abundance of brook trout have been correlated with the introduction of rainbow trout (Larson and Moore 1985; Strange and Habera 1998) and brown trout* Salmo trutta *(Waters 1983). Negative effects on the reproduction of brook trout caused by rainbow trout have also been documented (Moore et al. 1983; Larson and Moore 1985)."* (Isely and Kempton 2000, p. 613)

In general, the larger body sizes of introduced salmonines such as brown trout and rainbow trout have been associated with an edge in competitive interactions with native brook charr (Fausch and White 1986; Hearn 1987).

Competition for stream positions

Microhabitat use by steelhead tends to overlap most with brook charr soon after emergence of steelhead, when competitive interactions between steelhead and brook charr are likely to occur (Kocik and Jones 1999). Cunjak (1982) found that rainbow trout emergence appeared to cause a downward shift in the vertical position of brook charr in streams, and this has been interpreted as an indication of interspecific interaction in similar habitats (Kocik and Taylor 1995). For adults, it is probable that competition occurs between brown trout and brook charr for limiting areas of groundwater discharge and overhead cover (Kocik and Taylor 1995).

Fausch and White (1981) studied competition between brook charr and brown trout in the Au Sable River (Lake Huron) by measuring characteristics of stream positions held by brook charr before and after removal of brown trout. After brown trout removal, larger brook charr chose resting positions with more favourable water velocity and shade characteristics. The authors concluded that brown trout excluded brook charr from preferred resting positions, which the authors considered to be a critical and scarce resource in the river. Fausch and White (1981) also concluded that competition for resting positions, in combination with direct brown trout predation on juvenile brook charr, may have caused observed declines of brook charr in the Au Sable River watershed. This type of ecological release, resulting from addition or removal of a closely related species, is regarded as the strongest and most direct evidence to show interspecific competition for a resource (Diamond 1978; Sale 1979). It should be noted that the shifts observed by Fausch and White (1981) in positions of brook charr after removal of brown trout from a Michigan stream might have been due to the effect of electrofishing, for which there was no control, or due to changes in environmental factors during the study, which could not be assessed because sympatry and allopatry were not replicated (Fausch 1988).

In laboratory stream experiments with pairwise comparisons of coho salmon, brown trout and brook charr, Fausch and White (1986) showed that coho dominated brown trout and brook charr of equal size, and that brook charr dominated equal-sized brown trout. In these experiments, competitive superiority was based on the ability of fish to defend energetically profitable stream positions. When released from competition, the inferior species shifted to the more profitable positions; evidence of direct interference competition:

> *"We speculate that, as brown trout populations gradually increase, they spread through stream systems to points where they encounter shallowness, undesirably cold or warm temperatures, or other unfavorable conditions. At these limits of distribution, brown trout may be unable to compete successfully with brook trout for space, cover, or food. But in areas where physical conditions are suitable for both species, our results indicate that brown trout can exclude brook trout from preferred resting positions. Gaining these positions should allow brown trout growth and survival to increase at the expense of brook trout."* (Fausch and White 1981, p. 1226)

Fausch and White (1986) concluded that introduced adult brown trout successfully outcompeted brook charr for the most preferred stream habitats, making the charr more vulnerable to fishing and predation mortality.

Displacement of brook charr by rainbow trout has been suspected in many Great Lakes tributaries, where rainbow trout are typically more aggressive and are able to drive brook charr away from preferred areas in streams and rivers. As a result of this displacement, rainbow trout usually have access to greater quantities of food, leading in part to faster growth and larger body size than the brook charr (Krueger and May 1991).

Cunjak and Power (1986) investigated winter habitat utilization in brook charr and brown trout of the Credit River (Lake Ontario):

> *"Interspecific comparisons of winter habitat utilization at the two sites of sympatry indicate considerable overlap. Nyman (1970) and Fausch and White (1981) found that brook and brown trout have similar ecological demands, with brown trout usually dominating, often displacing brook trout to less optimal stream habitats. The numerical dominance of brown trout at the North Branch is probably a consequence of such competitive superiority and encroachment by this species since its introduction."* (Cunjak and Power 1986, p. 1978)

The authors concluded that both brook charr and brown trout preferred holding positions beneath submerged cover structures. Chapman (1966) considered habitat availability, of which cover is a major component, to be the primary regulator of salmonine population density during winter when low temperatures decrease the demand for food.

Competition for food

Peck (1974) found no substantial evidence of competition for food between yearling coho salmon and native species in a Lake Michigan tributary, however this evaluation is confounded by his own evidence: *"The insect and crustacean diet of emigrating juvenile coho placed them in direct competition for food with resident* *species of similar diet such as yellow perch (Dodge 1968) and spottail shiner (Basch 1968).*" (p. 14).

After emergence from the substrate, young introduced salmonines typically take up residence in the tributaries, where they may come into competition with young brook charr for space and food (Scott and Crossman 1973; Fausch and White 1986; Cada et al. 1987; Krueger and May 1991). Ensign et al. (1991) reported that brook charr and rainbow trout consumed similar diets, even in environments where they were sympatric. Rose (1986) presented evidence that juvenile steelhead suppressed growth of juvenile brook charr in a Lake Superior tributary, suggesting that this effect could be attributed to superior exploitative and interference competition for food. Taxonomic composition of the diets of the two species did not differ greatly; both fed primarily on juvenile aquatic dipterans, trichopterans, ephemeropterans and adult insects of various orders. Modelling by Clark and Rose (1997) has suggested that interspecific food competition between rainbow trout and brook charr during the juvenile period may have a significant influence on species composition in mixed populations. Johnson (1981) observed that the diet of brook charr overlapped substantially with hatchery steelhead, but less so with wild steelhead. Rose (1986) reported that, despite a later emergence date, steelhead offspring inhibited brook charr growth in a Lake Superior tributary, to the extent that the charr wintering mortality was significantly increased:

> "*Growth reduction during the first summer, an outcome of interspecific competition for food and space, may result in increased overwintering mortality of fish at high latitudes, and be a mechanism by which brook trout are excluded by rainbow trout.*" (Rose 1986, p. 187)

and

> "*The decreased growth of brook trout, linked with evidence of dietary and spatial overlap demonstrated in this study, is strong evidence of competition between [brook charr and rainbow trout] during their first summer. My data suggest that during June and July, when the more abundant rainbow trout co-occurred with brook trout, rainbow trout removed smaller food items in the stream drift which were previously available to the brook trout. Brook trout then fed on the remaining items that had sizes nearer the upper range available to them. This restriction of diet resulted in brook trout consuming less food. By late August, when rainbow trout had moved to sites with greater flows, brook trout had greater access to available food, and their stomach contents increased accordingly. In contrast, feeding by rainbow trout did not appear to be affected by the presence of brook trout.*" (Rose 1986, p. 191)

By the end of Rose's (1986) observations, rainbow trout were 50% more abundant than brook charr in the stream. Isely and Kempton (2000) examined the effects of costocking on the growth of juvenile brook charr and rainbow trout under experimental conditions with food in excess; they found that brook charr were significantly larger (length, weight) than rainbow trout when stocked alone, however rainbow trout were significantly larger than brook charr when they were stocked together. Isely and Kempton (2000) also commented that changes in environmental conditions would be expected to exaggerate this competitive asymmetry, especially under conditions of warmer water that would approach the optimum for rainbow trout. It should be noted that Cunjak and Green (1984, 1986), as well as Magoulick and Wilzbach (1998) observed the converse in other laboratory experiments. Whitworth and Strange (1983) observed a size advantage gained by rainbow trout over brook charr early in their second year of growth, and that this size advantage was continued throughout their lives.

Avery (1974) strongly suggested that juvenile coho salmon and steelhead competed with resident brook charr for available food and space in Wisconsin tributaries. Pre-spawning coho salmon in the Platte River (Lake Michigan) significantly decreased populations of 12 invertebrate species, thus reducing the availability of important food for the native predators (Hildebrand 1971). There is also evidence that Great Lakes brook charr are less competitive for food and cover, compared with coho salmon offspring which emerge earlier, and grow faster and larger (Gibson 1981; Fausch and White 1986). Coho salmon in Michigan streams have been shown to reduce brook charr populations through competition when food supplies are scarce (Taube 1975; Stauffer 1977).

Competition for food and space was shown to be a contributing factor for replacement of brook charr by brown trout in a Minnesota stream over a period of 15 years (Waters 1983). Growth and survival of brook charr in Michigan's Au Sable River in 1885 was observed to decline markedly after brown trout were introduced in 1891 (Smedley 1938 in Fausch and White 1981). DeWald and Witzbach (1992) presented evidence from experiments in which brook charr and brown trout were held alone and together in laboratory stream channels; they found:

(1) microhabitat location and vertical distribution of brook charr within the stream channels shifted in the presence of brown trout.

(2) the frequency with which the brook charr initiated aggressive interaction declined in the presence of brown trout.

(3) prey capture rates were higher for brown trout.

(4) brook charr lost weight in the presence of brown trout, which gained weight.

(5) in the presence of brown trout, 33% of brook charr contracted the fungus *Saprolegnia* sp. and died (brown trout were never infected, nor were brook charr in single-species trials).

Nyman (1970) observed no significant difference between stream-resident brook charr and brown trout, in the foods they selected. Coho salmon and brown trout are likely to compete with brook charr for food and space because of their similarity in juvenile life histories and ecologies in Great Lakes tributaries (Fausch and White 1986).

Competition for spawning habitat

All of the Pacific salmonines may compete with native brook charr (and other species) for spawning habitat in Great Lakes tributaries, even though the timing of spawning varies from species to species (Scott and Crossman 1973; MacCrimmon 1977; Krueger and May 1991). High quality spawning habitat in many Great Lakes tributaries is fully utilized where spawning Pacific salmonines are abundant (Kocik et al. 1991; Seelbach 1993; Kocik and Jones 1999). In many cases the larger, introduced spawning salmon are very aggressive towards stream-resident fishes; often interfering with the brook charrs' ability to seek forage and cover (Chapman 1962; Fausch and White 1986). During spawning preparations, the larger brown trout are aggressive to all intruders in their territory, including brook charr (MacKay 1969); however, this is not always the case:

> *"Although a potential time for confrontation between brook and brown trout is during the overlapping breeding season, our findings show surprisingly little species interaction at that time."* (Witzel and MacCrimmon 1983, p. 770)

Kocik (unpublished data cited in Kocik and Jones 1999) observed mature pink salmon attacking male brook charr and displacing them from female brook charr in spawning condition in a Lake Huron tributary.

Spawning requirements are virtually identical between brook charr and brown trout, with adults requiring gravel substrate and spawning occurring in October and November (Greeley 1932; Eddy and Surber 1960). Clapp et al. (1990) reported that brook charr and brown trout in the Au Sable River (Lake Huron) used the same spawning habitat. Witzel and MacCrimmon (1983) collected evidence from several southern Ontario tributaries (Lakes Huron and Erie) indicating that, despite some differences in redd-site selection, overlap existed between brook charr and brown trout spawning habitat. Brook charr spawned exclusively in areas of groundwater seepage (springs), whereas brown trout spawned in areas with and without groundwater seepage. Hansen (1975) reported that brown trout were observed to avoid groundwater upwelling, but overlap still remained. Unlike brook charr, brown trout and rainbow trout do not actively select groundwater seeps to spawn (Benson 1953; Sowden and Power 1985); however, rainbow trout embryo survival in redds is positively correlated with groundwater inflow (Sowden and Power 1985). Benson (1953) suggested that higher populations of brown trout at sites with greater groundwater inflow may be related to higher egg survival due to the groundwater. Bowlby and Roff (1986) suggested the same for southern Ontario streams.

Competition between introduced salmonines and lake charr

It is commonly assumed that different habitat preferences between lake charr and introduced salmonines would prevent intense competition for food (e.g., Scott and Crossman 1973; Olson et al. 1988). Olson et al. (1988) studied habitat distributions of lake charr, brown trout and chinook salmon in Lake Ontario during the summer; in this season, the salmonines were concentrated near shore where they apparently 'partitioned' available habitat and other resources. Horizontal habitat was 'partitioned' with respect to distance from shore; vertical habitat was 'partitioned' with respect to temperature and location of the thermocline. Evidently, salmonines foraged for the most available prey items in their habitat. Olson et al. (1988) reported that the percent overlap in horizontal distribution and food use was inversely related to percent overlap in vertical distribution; chinook salmon and brown trout used similar vertical habitats (78% overlap) but were segregated based on food types (15% overlap) and horizontal habitats (33% overlap). In contrast, lake charr and chinook salmon had a relatively high degree of overlap with respect to horizontal habitat (54%) and food types (70%), but lower overlap in vertical habitats (39%). Brown trout moderately overlapped lake charr on all three axes (45% food, 52% horizontal habitat, 50% vertical habitat). With respect to their diets: lake charr fed predominantly on smelt with some alewife, chinook salmon fed exclusively on smelt and brown trout fed predominantly on alewife and some smelt.

Competition for food

With introduced Great Lakes salmonines, spatial partitioning of food resources may be the exception, rather than the rule. For example, Aultman and Haynes (1993) found that Lake Ontario lake charr and chinook salmon were caught deeper than were coho salmon and steelhead, suggesting that the spatial partitioning described by Olson et al. (1988) was not occurring. Adult alewife normally concentrate at 11–14°C in Lakes Michigan and Ontario during thermal stratification (Brandt et al. 1980). Since both lake charr and salmon feed primarily on alewife, it can be inferred that both species overlap in space while foraging at or near the thermocline (Brandt 1986). Bioenergetic modelling for Lakes Michigan and Ontario presented by Mason et al. (1995) predicted maximal growth rate potentials for both lake charr and chinook salmon near the metalimnion, with highest prey fish densities in the epilimnion. In an application of bioenergetic models to a Lake Superior community, Negus (1992) estimated that introduced salmonines and lake charr were consuming more planktivores than were being produced, and that lake charr rations appeared to be at a critical minimum. Goyke and Brandt (1993) spatially modelled salmonine growth rate potentials for lake charr and chinook salmon in Lake Ontario, using distributions of predator and prey obtained from acoustic surveys. They found that both predators and prey occupied only a small fraction of the available habitat, with high degrees of overlap in growth potential between the two species. Negus (1995) argued that since rehabilitation of lake charr is a primary objective of the Great Lakes Fishery Commission, reductions in introduced salmonine stocking is a logical response to a limiting, common forage base (e.g., Mason et al. 1998).

In the open waters of the Great Lakes, introduced salmonines and lake charr may come into competition if prey availability is a limiting factor. Pacific salmonines in the Great Lakes, especially chinook salmon, have been shown to have diets similar to lake charr (Brandt 1986; Jude et al. 1987; Conner et al. 1993). For example, juvenile lake charr in Lake Ontario feed primarily on slimy sculpins and secondarily on alewife and rainbow smelt (Elrod 1983; Brandt 1986). All three of these species have been identified as receiving intense predation from both adult lake charr and introduced salmonines (Rybicki and Keller 1978; Crowder and Magnuson 1982). There have been indications of high diet overlap among lake charr, chinook salmon, Atlantic salmon and, to a lesser extent, coho salmon and rainbow trout (Negus 1995). Eck and Brown (1985) estimated that in 1979 alewife comprised 71% of Lake Michigan lake charr diets; similar estimates were obtained for coho salmon and chinook salmon (see also Stewart et al. 1981). Bioenergetic modellers have shown that while chinook salmon are widely known as voracious feeders, their lifetime forage is only about one-third more than the longer-lived and ecologically diverse lake charr (Stewart et al. 1981; Hansen et al. 1995). Chinook salmon sampled in Lake Michigan during conditions of cold water were found to have empty stomachs, while lake charr from the same region were found to have fed through the entire winter (Elliott 1993). Once again, these observations raise the question: was there really a need for biological control by introduced salmonines, when a native salmonine might have done the job?

It is important to note that local environmental conditions will always play a role in determining the competitive advantage between introduced and native rivals in the Great Lakes. For example, consider the case of rainbow trout in Lake Superior:

> *"The mean surface temperature of Lake Superior is less than 5°C for more than half the year (Phillips 1978), which is outside the normal thermal distribution of steelhead in its native range (Pauley et al. 1986). The harsh thermal regime of Lake Superior is less suitable for rainbow trout than for native species, such as lake trout, brook trout, and lake herring (Wismer and Christie 1987). Only time will reveal the level of sustainability for these populations, as all the species compete for food and habitat."* (Negus 1999, p. 939)

Under other circumstances, such as warmer waters of southern Great Lakes, the competitive advantage could be nullified or completely reversed.

Recently, investigators have begun to employ stable isotope analysis to explore the role of introduced salmonines in Great Lakes food webs:

> *"Introduced Pacific salmon occupied different trophic positions than native piscivores (lake trout, burbot). Exotic salmon in Lake Superior are a management concern because they are presumed to feed on the same prey resources as native piscivores, and the supply — demand relationship between these predators and the forage base is uncertain (Ebener 1995; Negus 1995). Our results suggest that chinook and coho salmon are lower on the food web than adult lake trout and burbot. If direct foraging competition between exotic and native piscivores exists, it may be between adult salmon and subadult native predators. Exotic salmon appear to rely upon rainbow smelt, which are important prey for young lake trout (Mason et al. 1998), and upon invertebrates, which are important to young lake trout and young burbot (Hansen et al. 1995; S. Schram, Wisconsin Department of Natural Resources, Bayfield, Wis., unpublished data). Adult lake trout and burbot make greater use of coregonids and sculpins than do Pacific salmon, according to our results and gut content analysis."* (Harvey and Kitchell 2000, p. 1401, my emphasis)

In this case the data showed that adult lake charr in Lake Superior were feeding more on lake herring and sculpins than the introduced salmonines; however it revealed the important possibility that interspecific food competition is occurring between the larger introduced salmonines and the smaller lake charr and burbot. Once again, when we start considering some of the basic characteristics of life-history and ecology, we see that the potential for competition between introduced salmonines and native Great Lakes species is much greater than simple diet overlap of adult fish.

Given that alewife and rainbow smelt are typically the most common prey of both lake charr and salmon, and that intensive stocking of introduced salmonines is capable of dramatically reducing the abundance of alewife and perhaps rainbow smelt (Stewart et al. 1981; Jude and Tesar 1985), it is very likely that lake charr and salmon would come into direct competition for prey (Brandt 1986; Jude et al. 1987; Diana 1990; Conner et al. 1993). Alewife (ages 0 and 1) were the only prey fish eaten in substantial quantities by both juvenile lake charr and introduced salmonines (especially brown trout and coho salmon) in Lake Ontario, and thus are a potential focus of competition (Elrod and O'Gorman 1991): *"If the alewife population declines to the point that production of young is severely curtailed, competition among salmonines for young alewives as food will intensify ..."* (Elrod and O'Gorman 1991, p. 301). In this context, it is important to recognize the role of alewife and smelt as forage in lake charr reintroduction programs (Argyle 1982). Elrod et al. (1995) commented that lake charr in Lake Ontario must "*share the lake's productive capacity with five other species of salmonine predators that are stocked to provide a sport fishery*" (Elrod et al. 1995, p. 105). Analyses of predatory demand by Ebener (1995*a*, unpublished manuscript cited by Mason et al. 1998) and by Negus (1995) indicated that, when considered together, populations of lake charr and stocked non-native salmonines in Lake Superior, may have exceeded the total carrying capacity of the ecosystem for top predators. If carrying capacity had been exceeded in this manner, it would be very difficult to imagine how lake charr and the non-native salmonines could not be in competition for limited food.

Finally, the issue of competition between native lake charr and introduced salmonines has recently been turned on its head, at least in the case of Lake Superior:

> *"Concern regarding impact of chinook salmon and other nonnative salmonines on lake trout in Lake Superior appears to have dissipated somewhat now that naturally reproducing lake trout stocks have been restored in much of the lake (Hansen et al. 1995). Naturally produced lake trout numbers increased during the late 1970s to early 1990s when chinook salmon stocking more than doubled in Lake Superior. In the 1990s, lean and siscowet varieties of lake trout were estimated to make up 93% of total predator biomass in the western third of the lake compared with 3% for chinook salmon (M. Ebener, Chippewa—Ottawa Treaty Fishery Management Authority, personal communication). If biomass composition is similar throughout the lake, it is doubtful that chinook salmon have any measurable effect on lake trout growth, even though they feed on the same prey fish and their gross conversion efficiency is greater (Conner et al. 1993; Ebener, personal communication). A greater likelihood is that increased lake trout abundance is responsible for decreased abundance of chinook salmon and other salmonines reported in parts of Lake Superior since the mid 1980s (Peck et al. 1994). If lake trout abundance continues to increase and they re-occupy their former habitats, there will be less food and room for chinook salmon and the other nonnative salmonines."* (Peck et al. 1999, p. 162)

Despite the contradictory reports that introduced salmonines are flourishing in other waters of Lake Superior (e.g., Peck et al. 1994, 1999), it is interesting to see the reverse spin that fisheries managers might be putting on the competitive interactions between native lake charr and the introduced salmonines — a native fish crowding out prized (introduced) game species in Lake Superior. "*Stocking reductions of different species in Lake Huron are being discussed. Some people have questioned why not reduce lake trout stocking rather than chinook salmon*" (LHMU 1998, p. 105):

> *"Indeed, before allocations of [Great Lakes] forage can be implemented, fishery managers must make difficult decisions on a higher level and address questions which have not all been answered. Do you allocate forage to lake trout rehabilitation, although stocked lake trout are not reproducing successfully, except in Lake Superior and several sites in Lake Huron (Selgeby et al. 1995)? Should efforts to rehabilitate lake trout be abandoned in favor of put-and-take planting of salmon? Do you allocate forage for salmonines, and hence, sport fisheries at the expense of commercial fisheries? How do you avoid the overstocking of chinook salmon (*Oncorhynchus tshawytscha*) that may have depressed the forage bases in Lakes Michigan and Ontario in the 1980s (O'Gorman and Stewart 1999)?"* (Brown et al. 1999, p. 363)

What would happen if fisheries agencies ever did finally succeed in rehabilitating a lake charr population elsewhere in the Great Lakes; would they be welcomed or would they be perceived as an competitive threat to the introduced salmonines and the sport fisheries?

Competition for spawning habitat

There is also evidence that at least one introduced salmonine engages in a form of direct interference competition for spawning habitat with lake charr in the Great Lakes. The Ontario Ministry of Natural Resources has evidence from one of the last surviving and reproducing populations of lake charr in Lake Huron (i.e., Iroquois Bay northeast of Manitoulin Island; Berst and Spangler 1973) indicating that lake charr on the spawning grounds were attacked by reproductively mature chinook salmon:

> *"Disturbance of redds and aggression between spawning chinook salmon and spawning lake trout are a possibility because the two species may be on the same shoal at the same time of year. During a winter creel survey of Iroquois Bay in 1985, the creel clerk noted that a number of lake trout larger than 0.9 kg had large scars on their sides. The scars were described as being more like deep scrapes than like lamprey scars. During spawn collection in 1985, the workers noted that 10 male and 1 female lake trout had unhealed wounds located on their sides posterior to the dorsal fin. In 1987, five of the lake trout captured had similar wounds. Although the origin of these wounds is unknown, aggression between chinook salmon, which averaged about 7 kg, and lake trout, which varied between about 1 and 6 kg, is a plausible explanation."* (Powell and Miller 1990, p. 243)

The Ontario Ministry of Natural Resources has additional evidence from 'spawning shoal surveys' for Iroquois Bay in the autumn of 1993:

> *"One important outcome emerging from the fall shoal survey was the observation that there may be competition between lake trout and chinook salmon for spawning shoals in Iroquois Bay. A large number of lake trout sampled during this survey bore fresh scars and open wounds that may have been inflicted by aggressive interactions with spawning chinook salmon. Similar observations were made during spawning shoal surveys in 1987. In the fall of 1987, chinook salmon in spawning condition were captured on a spawning shoal historically used by lake trout in Iroquois Bay. Divers observed numerous eggs and chinook salmon redds in the shoal area and a sample of these eggs were collected and incubated at a hatchery. Upon hatching, it was confirmed by both visual identification and genetic techniques that these offspring were indeed chinook salmon. These observations may prove to have significant management implications. The potential for natural reproduction by chinook salmon may be greatly increased. As well, there is a possibility of negative interactions between chinook salmon and lake trout on spawning shoals."* (LHMU 1994, p. 55)

and again in 1994:

> *"The observation of chinook salmon utilizing lake trout spawning shoals was repeated in 1994. In 1993, a total of 9 chinook salmon were captured in the vicinity of lake trout spawning shoals. The number of chinook salmon captured in 1994 increased to 36 and they were present at each of the spawning shoals being assessed. Four of the lake trout caught in 1994 (21%) showed evidence of*

> *fresh scars and wounds consistent with chinook salmon attacks.*" (LHMU 1995, p. 55)

Thus, there is accumulating evidence of direct interference competition between chinook salmon and individuals from one of the last two wild-reproducing populations of lake charr in all of Lake Huron. If these observations are an indication that introduced salmonines have shifted their life-history requirements (see Section 3.1.4) to enable spawning on traditional lake charr spawning grounds, then competition for access to spawning grounds could threaten any plans to rehabilitate lake charr in the Great Lakes.

Competition between introduced salmonines and other native species

There is evidence of potential competition for food between yellow perch and rainbow trout (Galbraith 1967; MacLean and Magnuson 1977), between coho and chinook salmon and walleye (Leach and Nepszy 1976; Brown et al. 1999). There is also evidence that introduced salmonines have competed with Atlantic salmon released as part of the re-introduction program in Lake Ontario. Jones and Stanfield (1993) evaluated the effect of age-1 and older steelhead, age-0 coho salmon and age-0 and older brown trout on Atlantic salmon juveniles in a Lake Ontario tributary. They observed that when the densities of these potential predators and competitors were reduced, the summer growth and survival of Atlantic salmon increased significantly. Jones and Stanfield (1993) suggested that, given the high degree of microhabitat overlap between age-0 Atlantic salmon and age-0 steelhead, once the latter reached 40 mm TL, the two species would come into competition that could affect the Atlantic salmon's juvenile growth and survival. It is also possible that Pacific salmonines and Atlantic salmon may compete for limiting spawning habitat in Lake Ontario tributaries (Kocik and Jones 1999). There is evidence indicating that late-autumn spawners (coho salmon) and spring spawners (steelhead) may superimpose their redds upon those of Atlantic salmon (Stanfield et al. 1995).

3.2.4 Genetic alteration

The first type of direct genetic effect documented for fish introductions is the creation of sterile hybrids (Schwartz 1972, 1981). In this case, the introduction of a non-native species effectively transcends geographic barriers that would otherwise have prevented hybridization, and may change the behavioural isolating mechanisms as well. Although evidence of hybridization among native and introduced fish species is relatively rare, the possibility of interaction is not insignificant (Taylor et al. 1984; Kohler and Courtenay 1986). Infertile interspecific hybrids resulting from such interaction can pose a competitive threat to the native species, and may also jeopardize population maintenance by distributing reproductive 'mules' that disrupt normal spawning activities. It should be noted that wild hybrids are often expected to be less fit than their parent species, however recent research has challenged the validity of this assumption (Arnold and Hodges 1995; Arnold 1997).

A second type of direct genetic effect is 'introgression'; the establishment of viable hybrids and the potential for transfer of the introduced species' genes into the gene pool of the native species (Schwartz 1972, 1981). Such a flow may disrupt the adaptive gene complexes which have evolved over time to provide a fit between the native species and its ecosystem (Philipp 1991). Introgression may be a serious ecological problem, long after hybridization ceases. Depending on the severity of introgression, the niche characteristics of the native species may shift so far as to pose a significant threat to survival. Various populations of a native species in an ecosystem may be highly adapted to local conditions. As a result, interbreeding with introduced fishes may reduce their ability to respond to important environmental fluctuations (Utter 1981; Meffe 1992; Li and Moyle 1993)[4].

Sorensen et al. (1995) argued that negative indirect consequences of attempted hybridization between brown trout and brook charr may be more important than the direct consequences. Attempted hybridization may reduce mating success of female brook charr by reducing the availability of male brook charr which are preferentially attracted to the larger brown trout females (Sorensen et al. 1995).

Previously, it had generally been accepted that the likelihood of wild hybrids occurring between salmonines was quite low, even in hatchery environments (Schwartz 1972; Chevassus 1979; Blanc and Chevassus 1986):

> *"Most diploid crosses of salmonine species produce no hybrids or weak individuals without the survival qualities of either species. The existence of these naturally occurring, typically infertile F1 hybrids is rare and short lived (no future generations), and therefore the ecological effects from their presence in fish communities is probably minimal."* (Krueger and May 1991, p. 71)

This evaluation of introgression may hold true for introduced and native salmonines in the Great Lakes; however, emerging observations continue to remind us that salmonine reproduction is characterized by surprises (e.g., Verspoor and Hammar 1991; Hawkins and Foote 1998). Smith (1992) presented evidence of introgression between pink salmon and chum salmon in their native range. Despite the observation that Pacific salmonines are relatively old and highly differentiated in an evolutionary sense (Smith 1992; Stearley and Smith 1993), it appears that reproductive barriers between them are actually incomplete (Rosenfield et al. 2000). In fact, some salmonines seem to have a propensity for introgression — especially in cases where geographic isolation precluded the evolutionary need for isolating mechanisms to prevent hybridization (Behnke 1992; Hawkins and Foote 1998).

Brown trout have been known to hybridize with brook charr (Fig. 37) under both artificial and wild conditions, leading to the creation of hybrids known as 'tiger

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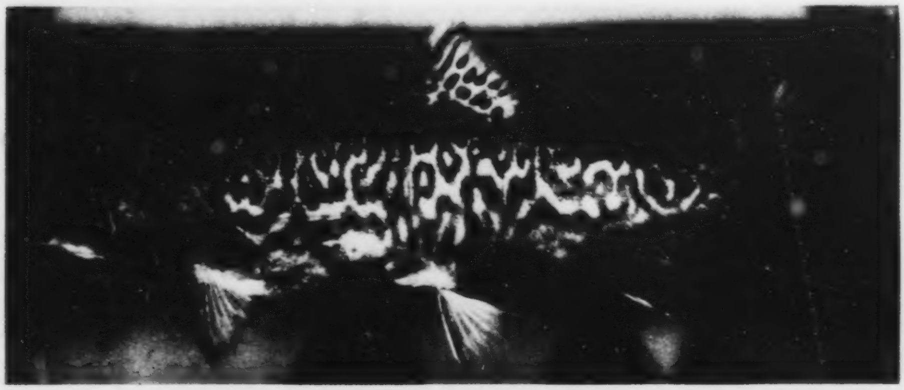
[4] As an interesting and ironic observation regarding the threat of genetic alteration perceived by Great Lakes fisheries managers, consider the caution raised with respect to the rainbow trout 'rehabilitation' program in Lake Superior:

> *"Two strains of anadromous rainbow trout* Oncorhynchus mykiss *currently inhabit the Minnesota waters of Lake Superior: (1) the steelhead strain, which was introduced in 1895 and has become naturalized, and (2) the "kamloops" strain (not the pure Kamloops strain from British Columbia, hence not capitalized), which was introduced in the late 1960s and has not yet been found to reproduce successfully in the wild (Krueger et al. 1994). Offspring of both strains are reared for supplemental stocking to satisfy public demands for a recreational fishery. Hybridization between the two strains is theoretically possible and may compromise the genetic integrity of the naturalized steelhead population. The importance of maintaining genetic integrity depends on the survival potential of each strain because the goal of managers is to rehabilitate the naturalized steelhead stock (MNDNR 1992; Schreiner 1995)."* (Negus 1999, p. 393, my emphasis)

Fig. 37. Wild tiger trout hybrid between introduced brown trout (*Salmo trutta*) and native brook charr (*Salvelinus fontinalis*). This specimen was collected by F.H. Marshall on the Bighead River (Lake Huron basin) in May 1979. Photo credit: Royal Ontario Museum (ROM 35744).



trout' (Allan 1977; Witzel 1983). The Illinois Department of Natural Resources actually stocked tiger trout into Lake Michigan during the period 1978–1980 (GLFC 2000). These hybrids have been reported to occur elsewhere in the wild (Waters 1983; Witzel 1983), especially where spawning habitat is intermediate between preferred conditions for brook charr (upwelling groundwater, relatively low water velocity) and brown trout (relatively high water velocities) (Sorensen et al. 1995). Such hybrids exhibit a striking pattern of marks (Fig. 37), and are typically quite stocky in body shape. Witzel and MacCrimmon (1983) reported the occurrence of wild tiger trout in Galt Creek (Lake Erie) and they commented on its rarity in the wild. It is thought that mortality of tiger trout during the early life-history periods is quite high (Scott and Crossman 1973).

Crossman and Buss (1966) reported the successful results of artificial hybridization between brook charr and kokanee. Dumas et al. (1992) reported on the creation of artificial hybrids between brook charr and Arctic charr — a species which has been the subject of cage culture operations in northern Lake Huron. There have also been observations in Valley Creek (a tributary to the St. Croix River in Minnesota) of attempted spawning between male brook charr, rainbow trout and brown trout, even though the rainbow trout females typically do not spawn until March (Sorensen et al. 1995).

There is abundant evidence of wild hybridization and introgression between Atlantic salmon and brown trout (both maternal directions) in Europe (Payne et al. 1972; Youngson et al. 1992, 1993; Jordan and Verspoor 1993; Hartley 1996; Jansson and Öst 1997) and in North America (Verspoor and Hammar 1991; McGowan and Davidson 1992). Verspoor (1988) observed widespread hybridization in Newfoundland rivers occurring at significantly higher frequencies than those observed in Europe; he suggested that less-discriminating behaviour of native Atlantic salmon and introduced brown trout could be an explanation for the observed difference in hybridization frequencies. The role of precociously mature Atlantic salmon parr had been suspected as being important in this hybridization, and this has been confirmed through experimental work in the wild by Gephard et al. (2000). Based on this evidence, it appears that wild hybridization between recently sympatric salmonines may be much more common and ecologically significant than previously supposed (Sorensen et al. 1995).

There is also evidence for hybridization among introduced salmonines in the Great Lakes. Hybridization occasionally occurs among these salmonines in their native sympatric range; for example, chinook salmon × coho salmon (Johnson and Ringler 1981; Bartley and Gall 1990; Bartley et al. 1990), pink salmon × chum salmon (Foerster 1935; Simon and Noble 1968) and rainbow trout × cutthroat trout (Campton and Utter 1985). In the latter case, the hybrid was shown to be capable of reproduction (Scott and Crossman 1973). Artificial crosses have been made between a variety of the introduced salmonines, for example: brown trout × rainbow trout (Buss and Wright 1956, 1958), kokanee × rainbow trout (Foerster 1935) and cutthroat and rainbow trout (Reinitz 1977, wild crosses reported by Hawkins and Foote 1998). Successful hybridization between coho salmon and rainbow trout has been reported under both artificial conditions (Ord et al. 1976) and wild conditions in the Great Lakes (Scott and Crossman 1973).

Recently, evidence has come to light about significant wild hybridization between pink salmon and chinook salmon (Fig. 38) in the Great Lakes. Rosenfield (1998) and Rosenfield et al. (2000) found evidence of wild hybridization and backcrossing between pink and chinook salmon from the St. Marys River (a connecting channel between Lakes Superior and Huron):

> *"If their recent hybridization in the Great Lakes leads to introgression, it could produce rapid change in one or both species For example, Leray et al. (1987) and Smith (1992) presented evidence that introgressive hybridization has played a role in the evolution of genus* Oncorhynchus. *Whereas introgression is common among less derived members of* Oncorhynchus *(e.g., Campton 1987; Allendorf and Leary 1988; Dowling and Childs 1992), among the five, more derived, Pacific salmon species it appears to be uncommon, and some evidence of resistance to introgression exists among theses species (e.g., May et al. 1975; Bartley et al. 1990). The fertility of hatchery-reared pink salmon × chinook salmon hybrid offspring (Foerster 1935; Chevassus 1979) demonstrates that introgression is possible between these two species."* (Rosenfield et al. 2000, p. 670)

The authors continued on to discuss the ecological significance of this wild hybridization among introduced salmonines, in relation to differences between the Pacific and Great Lakes ecosystems:

> *"Hybridization between pink salmon and chinook salmon is probably largely driven by differences between the physical conditions found in the Great Lakes drainage basin and those of the Pacific Coast watersheds these species normally inhabit (Rosenfield 1998). Salmon spawning migrations in the St. Marys River end at the Sault Ste. Marie locks, approximately 110 km from the river's mouth. At the foot of this barrier are rapids that constitute the only suitable mass-spawning grounds on the St. Marys River (other spawning grounds exist on its tributaries). This inability to migrate far upstream, combined with the limited salmonid spawning grounds in the main stem of the St. Marys River, probably forces spawning chinook and pink salmon into close proximity—a situation that rarely occurs in their native Pacific Coast habitats. Their placement*

> *in a novel evolutionary environment may explain why pink salmon and chinook salmon hybridize in the Great Lakes, but the frequency and directionality of that hybridization require additional study and explanation.*" (Rosenfield et al. 2000, p. 676)

Wild hybridization between these two species is all the more noteworthy because it represents a successful cross between two different subgroups within the genus (Domanico et al. 1997); an observation that increases the probability of crosses between less-distinctly related salmonine species.

Indirect genetic effects of fish introductions have more to do with changes in effective population abundance of a native species, and the effects that such changes have on the gene pool of the population. If abundance of a native population is reduced as a result of some ecological effect of a fish introduction (e.g., disease, predation), then the native population will display increased rates of genetic drift and inbreeding — which, in turn, can increase the frequency of negative alleles in the native population. In the case of brook charr, geographic displacement and confinement to tributary headwaters is thought to have reduced the overall genetic variability by impeding gene flow (Krueger and May 1991).

Fig. 38. Wild hybrid between pink salmon (*Oncorhynchus gorbuscha*) and chinook salmon (*Oncorhynchus tshawytscha*) captured in September 1996 at the mouth of Garden River; a tributary to the St. Marys River, which in turn is a connecting channel between Lake Superior and Lake Huron. Photo credit: Roger Greil, Mike McQuaid (photographer) and John Shibley, Lake Superior State University.

3.2.5 Environmental alteration

All species in a community alter their environment to some degree; however, introduced fishes may alter the recipient environment in a manner or degree unlike the existing native species (Li and Moyle 1993). The ecological effects resulting from such environmental alterations will vary, depending upon the particular environment and species involved.

Tributary substrate disruption

When salmonines spawn in a tributary, they typically do so after constructing redds within gravel substrate of the stream channel. If available areas for spawning are limited, later spawners may superimpose their redds on previously constructed redds, injuring or displacing embryos deposited by earlier spawners (Fukushima et al. 1998). Hayes (1987) found that the reproductive success of introduced brown trout in a small New Zealand tributary was reduced by more than 90% due to redd superimposition by later-spawning, introduced rainbow trout. Redd superimposition is frequently attributed to the limited availability of spawning habitat, perhaps because this behaviour has been extensively documented in anadromous salmonines which often face severe habitat limitations. However, Essington et al. (1998) experimentally tested this hypothesis in a Minnesota stream and they found that redd superimposition between brown trout and brook charr was not actually associated with habitat limitation. This evidence suggests that at least some salmonines may exhibit a preference to spawn where other fish had already spawned — an even more alarming situation for native fishes in Great Lakes tributary communities.

Many non-native salmonines in the Great Lakes basin have been reported to dig up or superimpose redds of earlier spawners, including native species (Avery 1974; Fausch and White 1986; Kocik and Taylor 1987b). Hildebrand (1971) used Burner's (1951) estimate of 2.8 m^2 of benthos disturbance area associated with each coho spawning redd to estimate that the 1967 spawning run on Platte River (51,574 spawner count) could have disturbed more than 14,000 m^2 of gravel during spawning. This kind of physical damage to native spawning beds is highly probable in many Great Lakes tributaries, especially where anadromous salmonine biomass is high and spawning habitat is limited (Kocik and Taylor 1995; see also Section 3.1.3).

Witzel and MacCrimmon (1983) observed that brook charr deposited their eggs in relatively shallow redds (i.e., <14 cm) compared to brown trout that dug much deeper redds (i.e., >14 cm). DeVries (1997) reviewed data indicating that brook charr typically bury their eggs in redds that are more shallow than the Atlantic and Pacific salmonines in the Great Lakes. Witzel and MacCrimmon (1983) suggested that reuse of brook charr redds by brown trout is probably modest, except where spawning densities are increased, such as below barriers to upstream movement. Redd excavation and superimposition by brown trout after brook charr spawning has been observed in a Minnesota stream (Sorensen et al. 1995). Evidence for the ecological effects of redd damage through substrate disruption has also been reported among introduced salmonines. Avery (1974) observed that most coho salmon spawned after resident brook charr, and they strongly suspected that destruction of brook charr redds by superimposition occurred. Kwain (1982) observed that pink salmon females superimposed their redds on those of other pink salmon that had previously spawned in that location. MacCrimmon and Gordon (1981) observed redd re-use, disruption and superimposition among coho salmon, rainbow trout and brown trout in Normandale Creek (Lake Erie). Kocik and Taylor (1995) suggested that steelhead redd superimposition could physically damage or displace brown trout from redds. In New Zealand tributaries, redd superimposition by rainbow trout has been shown to reduce the hatching rate of eggs of earlier spawning brown trout to less than 1% (Hayes 1987). Kocik and Taylor (1995) also argued that spawning overlap in Great Lakes tributaries could foster 'streambed overseeding' that could degrade the water quality of redd areas, adversely affecting survival of other stream residents.

Substrate disruption by introduced salmonines in Great Lakes tributaries also has direct ecological effects on the local aquatic community. The dislodgement and piling of gravel during redd construction can physically destroy habitat for other stream-resident fishes such as sculpins (Krueger and May 1991). Digging and cleaning activities of large, aggressive salmon can significantly reduce the abundance and production of invertebrate prey for a variety of native species, below levels characteristic of tributaries without introduced salmonines (Fausch and White 1986). An experimental investigation conducted by Hildebrand (1971) on the Platte River (Lake Michigan) demonstrated that coho spawning activities disturbed the bottom material and reduced the densities (66% of control), total numbers (66% of control) and total weights (78% of control) of 12 invertebrate taxa; significant reductions in these variables persisted for at least another five months following spawning. Hildebrand (1971) also observed that the swimming activity of these large fish disturbed the substrate with ongoing efects from October to November. Little, if any, available gravel in the river escaped this physical disturbance, and virtually all of the periphyton was removed from the substrate.

Tributary manipulation by humans

Physical stream manipulation by humans is a form of environmental alteration associated with the support of Great Lakes salmonine introductions, if not actually caused by the introduced fishes themselves. In virtually all cases, stream manipulation by humans is intended to increase the probability of successful reproduction and early survival of introduced salmonines in tributaries. In many cases, such stream projects are intended to remedy previous human disturbance of the streams (e.g., damming, deforestation, water pollution) in an attempt to 'rehabilitate' the stream ecosystem. However, in other cases, the intention is not to remedy previous human abuses of the environment but rather to 'improve' stream conditions to maximize production of introduced salmonines.

Stream 'improvement' to increase salmonine carrying capacity has been a common management practice since the 1930s (Greeley 1935; Needham 1936; Tarzwell 1936, 1938). These practices typically focus on increasing the cover, lowering stream temperature and stabilizing water flow (Kocik and Jones 1999). For example, Meyers et al. (1992) reported that high water temperatures and scarce spawning habitat in Beaver Creek (Lake Michigan) combined to limit the production of brown trout, and they called for habitat alteration to increase brown trout production. Alexander and Hansen (1983) reported a 40% increase in the abundance of young brown and rainbow trout after the removal of excess sand in a Lake Michigan tributary. In this case, the basic physical characteristics of the tributary were altered to increase production of an introduced salmonine (see also Mundie 1974). Another dramatic alteration of a tributary environment is the addition of gravel to create an environment more suited for intensive salmonine production. Avery (1996) reported that the State of Michigan maintained 166 sediment traps on 112 different streams, with the general result of increased salmonine production (see also Alexander and Hansen 1986). These manipulations may reverse human degradation to the stream environments; however, the singular focus of increased salmonine production poses risk to non-salmonine members of the aquatic community. This risk is particularly high in streams like many in Wisconsin which simply do not have large areas of gravel substrate, or historical evidence of significant salmonine reproduction (Avery 1996). In the end, it would appear that the motivation to maximize introduced salmonine production in Great Lakes tributaries has gone beyond environmental remediation, into the realm of environmental re-engineering (Devore and White 1978). Apparently, the risk of such environmental manipulations on native species in the community has not been investigated.

Toxic contaminant transport

The available evidence shows that introduced salmonines acquire significant contaminant loads (e.g., Mirex, PCB) in the open-lake environments via consumption of prey (but see Lamon and Stow 1999 for cautions about interpreting contamination trends through time). Of all the prey available to Lake Michigan salmonines, adult alewife have been shown to exhibit the highest PCB concentrations (Madenjian et al. 1993). Under normal circumstances, PCB accumulation by a predator increases as gross growth efficiency decreases. For example, initial gross growth efficiency is similar between rainbow trout and lake charr; however, gross growth efficiency decreases more rapidly with time in rainbow trout than in lake charr, indicating that PCB accumulation is higher in rainbow trout (Madenjian et al. 1994). Net trophic transfer efficiency for PCB in Lake Michigan coho salmon and rainbow trout has been estimated to be approximately 50% (Madenjian et al. 1994, 1998).

Quantitative models have indicated that the mistaken perception of higher PCB loading in lake charr compared to rainbow trout has to do with differences in age of recruitment to the sport fishery; rainbow trout at age 2–3, lake charr at age 5 (Madenjian et al. 1994). Jensen et al. (1982) demonstrated that 7.5% of PCBs in lake charr and salmon was transferred by direct uptake. Spigarelli et al. (1983) credited direct uptake for 10% of the total PCB accumulation in brown trout, and concluded that body contaminant burdens of the predators would equilibrate with the concentrations in their food supply in 70–155 days, depending on temperature. Farr and Blake (1979) presented evidence of Lake Ontario chinook and coho salmon that contained Mirex in concentrations exceeding health standards for human consumption. The 1976–1978 restrictions on possession of salmonines in New York waters of Lake Ontario were imposed as a public health precaution for this reason (Panek 1984).

Introduced salmonines release contaminants in Great Lakes tributaries by metabolic processes, egg deposition and carcass decay (Merna 1986; Eggold et al. 1996). Native species that eat eggs from contaminated spawning salmon can receive substantial burdens of pesticides (Fausch and White 1986; Merna 1986). Stauffer (1972) and Johnson and Ringler (1979*a*) found that brook charr and sculpins fed heavily on the eggs of introduced salmonines. Johnson and Ringler (1979*a*) suggested that other native species also may feed extensively on salmonine eggs, including: American eel, creek chub, fallfish, white sucker and northern hog sucker. In addition, invertebrate scavengers such as crayfish and amphipods are known to ingest contaminants in salmonine flesh (Merna 1986). Those eggs that are not eaten will release contaminants as they decay (Merna 1986).

Lewis and Makarewicz (1988) found that resident stream fishes (creek chub, smallmouth bass, bluntnose minnow) accumulated Mirex in a Lake Ontario tributary accessible to spawning runs of coho and chinook salmon. While coho and chinook salmon sampled in the accessible tributary had elevated levels of Mirex in their tissue, no Mirex was detected in white suckers, another anadromous species in the accessible tributary; this indicates that the principal source of the contaminant was the introduced salmonines. No such levels of Mirex were detected in tributaries with dams that prevented such salmonine migration. Direct transfer to stream resident species could occur by ingesting portions of the salmon carcasses (Fig. 39) or the eggs after spawning (Lewis and Makarewicz 1988).

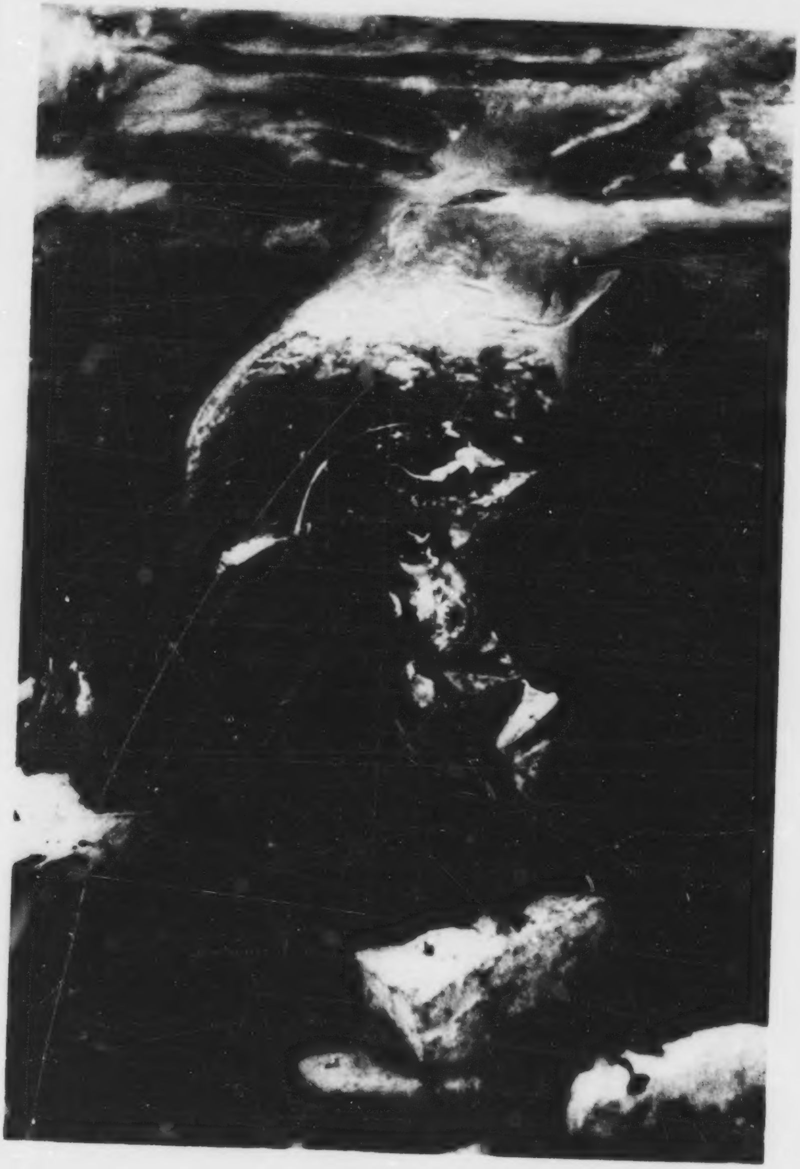
Low (1983) found that stream resident brown trout were contaminated with Mirex by exposure to spawning Pacific salmonines in the Salmon River (Lake Ontario). This uptake was attributed by the investigator to the ingestion of salmon eggs, and perhaps to post-mortality release of Mirex directly into the water and sediments. Scrudato and McDowell (1989) found that the migration of introduced salmonines in Lake Ontario was responsible for elevated levels of Mirex in the food webs of tributaries. They indicated that the mechanisms through which contaminants pass to native stream organisms included: ingestion of salmonine eggs, decomposition of salmonine carcasses by blowfly larvae (a primary terrestrial decomposer of salmonid carcasses, Fisher 1981) and ingestion of carcasses by aquatic (crayfish and stoneflies) and terrestrial scavengers. There is also evidence that Mirex transported by introduced salmonines enters the terrestrial food web from stream ecosystems (Johnson and Ringler 1979*a*; Low 1983; Leatherland 1993).

Merna (1986) provided evidence showing that introduced salmonines in Lake Michigan transport contaminants (e.g., PCB, DDT) to stream ecosystems, via the consumption of eggs and the decay of carcasses after spawning. This study provided strong evidence for chlorinated hydrocarbon contamination of resident stream trout by spawning salmonines in Great Lakes tributaries; however, the study failed to demonstrate retention of contaminants in stream sediments and indicated relatively low contamination of crayfish and sculpins. The observed food habits of the trout indicate that the most likely source of contamination was salmon eggs.

Hatchery effluents

Another indirect manner by which introduced salmonine stocking programs alter the Great Lakes environment is via the effluence generated by hatchery facilities (Szluha 1974). Salmon hatchery effluents have been investigated in Washington State streams; the ecological effects associated with these effluents included significant changes in water temperature, pH, suspended solids, ammonia, organic nitrogen, total P, chemical oxygen demand and effects on benthic invertebrate communities (Kendra 1991). Clark et al. (1980) made reference to closure of the Grayling fish hatchery by the State of Michigan, the consequent reduction of waste discharge on the Au Sable River (Lake Huron) and the possibility that effluent nutrients had been artificially accelerating the eutrophication of the tributary ecosystem.

Fig. 39. Chinook salmon (*Oncorhynchus tshawytscha*) carcass decomposing in Orono Creek (Wilmot's Creek watershed, Lake Ontario basin) in October 2000. Despite the small size of this tributary, more than 200 carcasses were observed by the author along a 300 m stretch — most of which were large individuals in the 10–15 kg range. Laurentian Great Lakes tributary ecosystems did not evolve with introduced salmonine species that undertake massive upstream spawning migrations, followed by one-time spawning (semelparity), mortality, decomposition and massive influx of biomass, nutrients and contaminants to the watershed. Photo credit: Kevin Judge.



3.2.6 Community alteration

Community changes caused by introduced fish species are associated with two well-established theories: the theory of island biogeography and the theory of limiting similarity. Together, these ecological theories predict four types of possible effects that a fish introduction may have on the niche characteristics of species in the receiving ecosystem (adapted from Li and Moyle 1993): (1) no niche compression of any species, (2) partial niche compression of similar species, (3) complete niche compression (extinction) of similar species, and (4) partial or complete niche compression (extinction) of dissimilar species via indirect and direct alterations of the environment or food web.

For the purposes of this subsection, I will present information on suspected or known effects of introduced salmonines on Great Lakes communities from two different perspectives:

- Effects of introduced salmonines on community composition
- Effects of introduced salmonines on community energetics

The first of these categories deals with the structure and function of communities at the level of species, while the second category deals with the structure and function of communities at the level of energy transfer.

Community composition

Gido and Brown (1999) and Rahel (2000) have reported on the homogenization of fish faunas in U.S. states due to the widespread intentional introductions of "*a group of cosmopolitan species*" of fish intended to enhance fisheries. These authors concluded that the most significant ecological effects were observed in areas with fewer indigenous species considered 'desirable' by a European-based sportfishing culture. Townsend (1996) reported that intentional brown trout introductions to New Zealand resulted in significant effects on the abundance and distribution of indigenous algae, invertebrates and fishes, and in the local extinction and fragmentation of native fish species with similar ecological requirements.

I have already discussed evidence of predation and competition between the open-lake salmonines and lake charr, especially with respect to food supply for juveniles and adults (Brandt et al. 1980; Elrod 1983; Brandt 1986; Diana 1990) and competition for spawning grounds. The brook charr has been widely displaced and reduced in abundance by stream-resident brown trout and rainbow trout, as well as by other introduced salmonines that migrate up the tributaries on spawning runs (Metzelaar 1929;Greeley 1932; Eddy and Surber 1960; Nyman 1970; Johnson 1980; Waters 1983; Krueger and May 1991). At the very least, it is clear that competitive interactions resulting from salmonine introductions can result in the compression of niche characteristics of the native charrs.

Reduction in abundance or extinction of similar species through competition is an extreme extension of the partial effects described in the preceding paragraph (see also Lassuy 1995). Such an effect would result in the local, and possibly basin-wide, disappearance of the species from the Great Lakes community. While no investigator has provided direct evidence that niche overlap was responsible for local extinction of brook charr populations around the Great Lakes, this may indeed have already occurred — quite frankly, we haven't really been looking. Similarly, it could very well have been competition with introduced salmonines that contributed to other changes (e.g., habitat degradation, over-exploitation) that resulted in local extinctions. The general failure of early salmonine introductions suggests that competition was probably not a significantly contributing factor to the initial demise of lake charr in the Great Lakes. However, it is quite possible that recent salmonine introductions interfere directly, or indirectly, with the re-establishment of lake charr populations.

There is one example in the history of Great Lakes salmonine introductions in which an introduced salmonine was held responsible — at least in part — for extinction of a native salmonid. The Great Lakes grayling (Table 1), which was originally abundant in Michigan tributaries with habitat requirements very similar to brook charr, became extinct in the late 1930s. Introduced brown and rainbow trout have been cited as contributing to the extinction of the grayling through both competition and predation (Hubbs and Lagler 1958; Vincent 1962).

Reduction in abundance or extinction of dissimilar species via indirect and direct alterations of the environment or food web can be considered the 'Pandora's Box' of the Great Lakes. Due to the complex and interdependent nature of such a community, it is unlikely that strong effects on one component of the system can occur without having profound effects on many other components. For example, Jude and Leach (1993) have argued that modern Great Lakes fish assemblages consist largely of pelagic species, whereas 200 years ago nearshore littoral communities were in an equilibrium state with pelagic offshore communities (see also Regier and Kay 1996). Similarly, Scavia et al. (1986) suggested that the introduction of salmonine predators, coupled with climatic changes, have drastically altered the trophic structure of Lake Michigan. In Lake Michigan, many of the changes in trophic structure have been attributed to the cascading, indirect effects of salmonine introductions such as the intense predation on alewife (Stewart et al. 1981). Reduced densities of alewife released predation on large zooplankton, and triggered a dramatic increase in large-bodied zooplankton (Evans and Jude 1986). Potential competitors of alewife, such as yellow perch, bloater and rainbow smelt also increased in abundance (Jude and Tesar 1985). Therefore, something apparently as simple as stocking non-native salmonines, can have complex ramifications far beyond the intended prey base. These changes may be considered desirable by some fisheries managers, yet undesirable by others. From an ecological perspective, these changes are less than desirable in the sense that they result from unguarded top-down tinkering with a complex community, without appropriate knowledge concerning the effects on ecological characteristics of native species (Koonce 1995).

With reference to the life-history characteristics of the dominant piscivore in the Great Lakes, some authors have suggested that both the iteroparity and longevity of lake charr contribute more to 'stability' of the ecosystem, relative to the typical semelparity and shorter lives of the introduced salmonines:

> *"It is no accident that all important Great Lakes native fish taxa are iteroparous (in contrast with the semelparous Pacific salmon), requiring more than a single spawning to replace the parental stock. So too are the invading species that have become self-sustaining. ... We concur with Christie and Regier (1972) that sustainability of a particular suite of species must be closely tied to a reproductive control investment that crosses a number of years. ... Collapsing the breadth of the age distribution of spawners for iteroparous species clearly limits the*

> *opportunities for such species to recover from otherwise benign enjuvenation events such as those due to local weather.*" (Christie et al. 1987, p. 494)

and

> "*Sizes of introduced salmonines are within the range of the historically dominant native piscivore, the lake trout, but they are shorter-lived species (Stewart et al. 1981) with higher P/B ratios, a factor associated with reduced sustainability. Coho and chinook salmon, steelhead, and brown trout, all intensively stocked, seldom exceed an age of five years, whereas lake trout commonly exceed an age of twenty years (Martin and Olver 1980).*" (Eshenroder and Burnham-Curtis 1999, p. 159)

With respect to longevity, Eshenroder and Burnham-Curtis (1999) commented that introduced salmonines are not as well-suited as native lake charr to be dominant piscivores in the Great Lakes — 2 or 3 consecutive years of poor recruitment and they would be extremely vulnerable. Longer-lived piscivores such as native lake charr can effectively 'store' periodic reproductive success that contributes to the 'stability' of their communities (Evans et al. 1987). With respect to iteroparity, recent investigations have shown that chinook salmon under hatchery environments have demonstrated the ability for iteroparous reproduction at ages 1, 2 and 3 years (Unwin et al. 1999). This observation raises the logical possibility that such a life-history shift could still be exhibited by introduced salmonines in the Great Lakes in the future.

Community energetics

Biological energy generated by primary producers (e.g., algae and plants) is the major currency of most ecological communities. By examining the distribution and flow of matter and energy, biologists are able to evaluate the persistence of ecological processes that shape these communities. One conspicuous transmission of energy associated with Atlantic and Pacific salmonines is the massive influx of organic matter and nutrients that are transported from lacustrine environments to tributaries during anadromous spawning migrations (Richey et al. 1975; Bilby et al. 1996, 1998; Cedarholm et al. 1999); this is especially obvious in oligotrophic waters such as those characteristic of natural Great Lakes watersheds. In addition to changes in gross energy budgets, introduced salmonines also have the potential to severely distort the flow of energy throughout the receiving aquatic and terrestrial ecosystems (Cedarholm et al. 1999). Flecker and Townsend (1994) conducted field experiments to compare the relative effects of introduced brown trout on the structure of a New Zealand stream community; they detected major perturbations that cascaded through the trophic web, ranging from insect distribution/abundance to the standing crop of aquatic primary production (see also McIntosh and Townsend 1994).

Introduced salmonines have been implicated in disruptions of energy pathways in both open-lake waters and tributaries of the Great Lakes. Recent work in the particle-size distribution of biomass in the Great Lakes has revealed some startling effects of introduced salmonines. For example:

> "*Indicators of ecosystem function have not been applied systematically to the Great Lakes, but some studies hint at continuing problems. Biomass size spectrum studies of Lake Michigan (Sprules et al. 1991) have shown promising results for the use of particle-size spectra in analyzing food web structure. Through this analysis, Sprules et al. (1991) found that piscivore biomass was*

> *lower than they expected. The imbalance in the food web appears to be limited availability of prey fish production to the mix of stocked piscivore species. Zooplankton size distribution, as a component of the biomass size spectrum, also indicates imbalance between planktivory and piscivory. According to the Lake Ontario Pelagic Health Indicator Committee (Christie 1993), a mean zooplankton size of 0.8 to 1.2 mm shows a healthy balance in the fish community. Over the period 1981 to 1986, the observed range of mean size of zooplankton was 0.28 to 0.67 mm (Johannsson and O'Gorman 1991), indicating excess planktivory. Emerging evidence for 1993, however, suggests that Lake Ontario may be undergoing an abrupt shift in zooplankton size with a collapse of the dominant prey fish population (E. L. Mills, Cornell University, personal communication). The recent trends in Lake Michigan and Lake Ontario may indicate that declines in productivity of both lakes associated with reduced phosphorus loading make these systems less able to sustain predator stocking levels that were successful earlier. Recent modelling studies of Lake Michigan and Lake Ontario (Stewart and Ibarra 1991; and Jones et al. 1993) indicate a strong possibility that excessive stocking of predators is de-stabilizing the food webs in these ecosystems."* (Koonce 1995)

Thus, it appears that introduced salmonines may have highly disruptive effects on the transfer and cycling of energy in the open waters of the Great Lakes (Coblentz 1990). Such energy disruptions are not restricted to the open waters, but are transferred via regular, and often massive, spawning runs up the tributaries (Krueger and May 1991; Gresh et al. 2000). These salmonine spawning runs are, with the exception of Atlantic salmon in Lake Ontario, typically not part of the ecological history of the Great Lakes. It should be noted that spawning migrations of introduced salmonines can reach substantial proportions. For example, numbers of steelhead returning to Great Lakes tributaries on spawning runs ranges from fewer than 1,500 to 15,000 or more (Kwain 1981; Karges 1987; Seelbach 1993). Some researchers have commented on the general ecological effects of introduced salmonine spawning runs in the Great Lakes:

> *"Discussing the migration and spawning of the salmon, Needham*[141] *says: "The end of the migration is not a pretty one. Weakened by the long trip from the ocean, by nest-digging and mating, scarred by fighting and covered with patches of dank, grey fungus, they die in the shallows, or are killed by birds and other predators, once they have filled their debt to nature."* (MacKay 1969, p. 72)

> *"Unlike the native lake trout or even the exotic rainbow and brown trout, natural post-spawning deaths of the coho salmon may leave the bottoms of breeding areas littered with decomposing cadavers which create disposal problems previously unknown to Great Lakes fishery managers."* (MacCrimmon 1977, p. 139)

The phenomenon of post-spawning mortality is typical of the Pacific salmonines (Fig. 39), with the exception of rainbow trout (Scott and Crossman 1973; Stearley 1992). It should be noted that Pacific tributaries have evolved aquatic and terrestrial communities which are adapted to — even dependent upon — this massive influx of salmonine matter (Teel et al. 2000); Great Lakes tributaries have not.

The community energetic effects of salmonine spawning migrations have been receiving growing attention from an ecological perspective, and there are a few studies that warrant special consideration. Johnson (1978) observed high abundance of crayfish in certain tributaries, and he suggested that this high production was related to the great abundance of Pacific salmonine carcasses that accumulated after the spawning runs. Johnson (1981) noted that perlid stonefly nymphs fed on salmonine embryos in the gravel redds, and suggested that these stoneflies could become superabundant on the basis of an abundant food source. Salmon carcass consumption has also been reported for blowfly larvae and terrestrial vertebrate scavengers (Fisher 1981; Cederholm and Peterson 1985; Cederholm et al. 1989). Johnson and Ringler (1979*a*, *b*) reported that salmon eggs and blow-fly larvae from decomposing salmon carcasses pose a significant contribution to the diet of juvenile salmonines in tributaries during the autumn.

In two Lake Ontario tributaries that are anthropogenically eutrophic (i.e., nutrients not limiting primary productivity due to human-based runoff), phosphorous release from chinook and coho salmon carcasses was estimated to be very low on an annual basis (i.e., <1%), but of higher importance (>50%) during the spring (Rand et al. 1992). Salmonine carcasses in Lake Ontario tributaries often overwinter in a near-frozen condition and much of the decomposition occurs after snowmelt during the following spring (Johnson and Ringler 1979a; Fisher 1981). Parmenter and Lamarra (1991) reported that 95% of accessible salmon carcass nitrogen (N) and 60% of accessible carcass phosphorous (P) were leached into the water column within 10 months of death. It is likely that the relative impact of nutrient loading from salmon carcasses would be much more pronounced in oligotrophic streams (Fisher Wold and Hershey 1999; see also Gresh et al. 2000), such as those found in natural Great Lakes tributaries. Allen and Hershey (1996) reported seasonal N and P limitations on instream primary productivity in a Lake Superior tributary. Schuldt and Hershey (1995) demonstrated significant increases in primary productivity after the controlled addition of introduced salmonine carcasses to Lake Superior rivers and streams.

> *"Salmon carcasses decompose in north shore [Lake Superior] streams allowing their nutrients to become available to other stream organisms. We have demonstrated that nutrients derived from salmon carcasses can ameliorate nutrient limitation in the Little Knife River at small spatial scales even at low temperatures. The fact that we see a response to carcass decomposition when fish densities are orders of magnitude smaller than west coast salmon runs implies that even small amounts of added nutrients can have an important local effect on nutrient-limited streams."* (Fisher Wold and Hershey 1999, p. 772)

Clearly, there is a tremendous amount of biological energy that is abnormally transferred by introduced salmonines to Great Lakes tributaries during spawning runs. For local environments other than those already polluted with municipal–agricultural–industrial nutrients, salmon carcasses can significantly accelerate the eutrophication of Great Lakes streams and rivers.

Salmon carcasses have also been shown to contribute significant amounts of phosphorous to rivers and lakes elsewhere. Donaldson (1967) concluded that the total phosphorous originating from the 1965 escapement of sockeye into Iliamna Lake (Alaska) was 1.37 times greater than the total annual phosphorous contribution from all other sources combined. Krohkin (1967) found that almost 40% of the total phosphorous input in Lake Dalnee in Asia originated from post-spawning sockeye carcasses. Gresh et al. (2000) concluded that carcass decomposition in Pacific northeast has significant effects on tributary energy budgets through channels of primary (e.g., algae), secondary (e.g., invertebrates) and higher ecological production (see also

Kline et al. 1990; Minshall et al. 1991; Larkin and Slaney 1997; Wipfli and Caouette 1998).

In general, the introduction of salmonines through continued stocking can be considered a destabilizing force in the community energetics of the Great Lakes ecosystem — a force which, in contrast to the alewife, is a result of intentional and ongoing introductions by humans. Although some of these salmonines reproduce in the wild, recruitment to many Great Lakes populations is maintained primarily by annual plantings of hatchery-reared fish (see Section 3.1.3). These plantings are largely, if not completely, dissociated from considerations of ecological productivity in the receiving ecosystems (Eck and Wells 1983; Eck and Brown 1985):

> *"The early optimism about the future of the sport fishery generated during the late 1970s and early 1980s was tempered by observed signs of ecological stress in the salmonine community in Lake Michigan, predicted initially by Stewart et al. (1981) and later recounted by Kitchell and Crowder (1986) and Stewart and Ibarra (1991). The hypotheses put forth by these investigators state that predatory salmonines have the potential to depress pelagic prey fish abundance, and hence, create conditions where prey fish become limiting, resulting in reductions in predator growth, condition, and survival."* (Rand and Stewart 1998*b*, p. 318)

Serious concerns continue to be expressed regarding the overabundance of terminal predators in the Great Lakes, especially the introduced salmonines, relative to the ability of the ecosystem to support them (Edwards et al. 1990; LHMU 1998; Ford and Lonzarich 2000).

Intensive stocking of introduced salmonines may also have profoundly affected the growth rates and abundance of parasitic sea lamprey that depend heavily on the native and introduced salmonine populations in the Great Lakes (e.g., Lawrie 1970; Smith 1970). Consider the following comments with respect to the possible effects of stocking introduced salmonines in Lake Ontario:

> *"Following the initial small plants of chinook and coho salmon by the Province of Ontario in 1968 and New York State in 1970, stocking increased steadily, and in 1978 more than 2.4 million trout and salmon were planted in Canadian and United States waters of Lake Ontario (Great Lakes Fishery Commission, March, 1979, mimeograph). The resultant large salmonid base in the lake, coupled with the chemical control program, undoubtedly contributed to the recent increases in sea lamprey growth [rates]."* (Heinrich et al. 1980, p. 1869)

These kinds of observations stimulate challenging questions about the intention, approach, ecological-effectiveness and cost-effectiveness of both the salmon stocking and sea lamprey control programs in the Great Lakes drainage basin.

Stewart and Ibarra (1991) presented model projections for Lake Michigan indicating that modern stocking rates could yield introduced salmonine populations that would be more than four times as abundant as native lake charr. It is important to note that introduced salmonines are usually considered pelagic piscivores, while lake charr are piscivores that forage in both pelagic and benthic environments. Stocking strategies, such as those in Lakes Ontario and Huron, produce a top predator that is at high risk of short-term changes in recruitment. Successive years of poor recruitment could effectively eliminate any of the introduced salmonines as a dominant species in the lake communities. Just such a loss began to occur in Lake Michigan when chinook salmon began to decline drastically in 1987, in association with an outbreak of bacterial kidney disease (Nelson and Hnath 1990). However, lake charr in Lake Michigan maintained their abundance and condition, even as chinook salmon populations declined (Rand et al. 1994). In Lake Superior, when smelt populations declined, so did chinook salmon; yet lake charr maintained their condition and became the dominant piscivore in the community (Peck et al. 1994; see also LHMU 1998). These observations suggest that, despite continued attempts to force introduced salmonines into the Great Lakes ecosystem, they may not match the ecosystem well enough to persist.

To understand the dependence of introduced salmonines on the planktivorous Great Lakes fishes, it is necessary to contrast their foraging abilities with those of the dominant predator that evolved within the ecosystem. None of the salmonines introduced to the Great Lakes seem to have been very successful predators on the deepwater forage species such as *Mysis relicta*, *Pontoporeia hoyi*, or adult bloater (Stewart et al. 1981) — however, these trends may be changing dramatically in response to food shortages (see Section 3.2.3). Inability to forage effectively on native prey may be due to a lack of co-evolution with these species. For example, consider the inability of sight-feeding Pacific salmonines to efficiently locate prey when they migrate to upper pelagic waters at night; *Mysis* would also be available to the introduced salmonines during daylight hours, except that these fishes do not apparently exhibit a great ability for hypoliminetic foraging (Eshenroder et al. 1995). Thus, there are historically important linkages between deepwater, offshore production and the remainder of Great Lakes trophic webs which apparently have not been established by the introduced salmonines (Argyle 1992; Elliott 1993). This lack of connectedness with Great Lakes ecological productivity is possibly a key reason for the observed declines in growth and survival of the introduced salmonines.

Historically, lake charr foraged effectively on the production of the deepwater invertebrate *Mysis*; a species which served as an important connection between different components within the Great Lakes community. In comparison, the introduced salmonines have shorter life-cycles than lake charr, and have a higher ratio of energy consumption to biomass (Stewart et al. 1981; Eshenroder et al. 1995). There is also evidence that introduced salmonines do not forage as effectively as lake charr, during winter months (Elliott 1993). When combined, these factors could lead to altered destinations and flow rates of energy within the ecosystem. These alterations, in turn, could be associated with reduced sustainability of introduced salmonines in the Great Lakes ecosystem.

Current management practices supporting introduced salmonines in the Great Lakes impose a destabilizing effect on the properties of the ecosystem as a whole. The recent replacement of non-native planktivorous species (i.e., alewife, rainbow smelt) with native planktivores in Lake Superior (Hansen 1994) and the recent recovery of burbot in Lakes Huron and Michigan (Eck and Wells 1987) provide strong support for the idea that the succession of native species-complexes is a basic property of the Great Lakes ecosystem.

4
Discussion

"There is a long and honorable tradition in western culture, dating back at least to the Romans, of tinkering with fish faunas by adding new species. This tinkering is part of a much broader tradition of tinkering with nature, to "improve" on it. The moral and mechanical problems that are encountered when trying to improve on nature were dramatically illustrated in Mary Shelley's famous novel, published in 1818, "Frankenstein, or the Modern Prometheus." In this story, Count Frankenstein, a dedicated scientist, attempts to create an improved human being but soon discovers, to his mortal distress, that he has created more problems than he has solved. Most of his problems stemmed from focussing on the solution to a narrowly perceived problem without considering how the solution (the monster) would fit into society at large." **(Moyle et al. 1986, p. 415)**

If we are going to make informed decisions regarding salmonine introductions in the Great Lakes, we need to understand the history and ecological effects of these activities. It is crucial that we understand how our attitudes and values regarding fisheries have been shaped over time, and that we learn from our past (Bocking 1997; Rahel 1997). It is for this reason that I return to advice I received from an historian colleague:

> *"... it is important to remember that:*
>
> *(a) hindsight is not foresight,*
>
> *(b) economic and social considerations dominate powerful decision-makers until grounds to prefer other criteria are convincingly established, and*
>
> *(c) historical and ecological change are irreversible.*
>
> *In other words, we can learn little from past experience if we assume people then shared the values of today's ecologists and criticize them for failure to apply those priorities; nor can biologists or anyone else simply go back and start over."* (R. Hoffmann, York University, personal communication, 1997)

From the beginning, salmonine introductions have been a response to the symptoms of our problems (i.e., shortage of desired fish, abundance of undesired fish), rather than the treatment of the problems themselves (i.e., habitat degradation, canal construction, overexploitation). Samuel Wilmot's fish-breeding establishment at Newcastle (Figs. 3–11) was more significant than just being the first government-operated hatchery in North America. It symbolized both the anthropogenic collapse of native salmonines in the Great Lakes and the response of European thinking; the belief that artificial measures can, and should, be employed to achieve human objectives in wild ecosystems (Livingston 1994). At the time, hatchery operators were apparently unaware of the negative ecological effects. Strangely, this form of fisheries management has remained a prevalent force in Great Lakes fisheries management.

The objectives for salmonine introductions to the Great Lakes have never been well-articulated. Originally, introduced salmonines were stocked for production of food, commerce and recreation. Later, in response to the exploding population growth of alewife and rainbow smelt, fisheries managers developed more sophisticated objectives of biological control — to treat the symptoms of yet another problem that humans had created.

A major question regarding the modern objectives for introduced salmonines is associated with the ranking of management priorities. Consider the following statement regarding the role of introduced salmonines in the Great Lakes:

> *"Stocking salmon to control alewives can be viewed as an end in itself with the additional economic and recreational benefits of a world-renowned sport fishery. It can also be viewed as a stopgap measure along a road to rehabilitation of the ecosystem. We are seeing the revival of native species and a substantial decline in alewife populations in Lakes Michigan and Huron."* (Jude and Leach 1993, p. 534)

According to this interpretation, the biological control objective for Great Lakes salmonine introductions seems to be the principal objective, with the recreational fishery objective serving in a subsidiary and auxiliary capacity. But read on ...

> *"An alewife population decline will have far-reaching effects throughout the lake and has the potential to impact the sport fishery as well. In fact, during 1993, in response to lower abundance and poor growth of alewives and rainbow smelt, substantial stocking reductions (>50%) were made for chinook salmon and lake trout."* (Jude and Leach 1993, p. 533)

Recall that alewife used to be portrayed as the 'bad guys' in Great Lakes fish communities; invaders with explosive potential that destabilized community dynamics by capturing huge amounts of energy, without being effectively converted into top-predator 'game' fishes. This undesirable situation supposedly required the introduction of non-native salmonines to control alewife abundance.

However, according to the actions of Great Lakes fisheries managers, it is clear that the only primary objective for introduced salmonines is to support recreational fisheries. We can reject the stated biological control objectives by examining statements made on the economic status of alewife:

> *"In an economic analysis of the allocation of Lake Michigan alewife to commercial (harvest for pet food) or sport fishery (prey for salmonines) interests, the commercial value was near 0, while the marginal net social value was $4.10 per salmonine, strongly suggesting alewives should not be harvested by commercial fishers (Samples and Bishop 1987)."* (Jude and Leach 1993, p. 534)

In this case, effective techniques for removal of alewife (i.e., commercial harvest) would actually be considered an indirect threat to the recreational fisheries, rather than as a complementary biological control technique (see also Keller et al. 1989; Brown et al. 1999). Digging a bit deeper into this issue, consider the alewife of Lake Ontario:

> *"Concern by the public and fisheries agencies over the decline of the alewife as a source of prey for stocked non-native salmonids (*Oncorhynchus *sp. and* Salmo *sp.) has caused NYDEC and the Ontario Ministry of Natural Resources to reduce stocking of salmonids (including lake trout) in an effort to ensure that alewives remain abundant (Lange and Smith 1995). In light of the present study, lakewide management seems headed away from restoration of native species toward managing for healthy populations of exotic prey species through reductions in stocking predatory salmonids."* (Krueger et al. 1995, p. 467)

Biological control has somehow 'mutated' into a fish feeding program to support a recreational fishery:

> *"Angling fisheries have expanded greatly in recent years as increasing numbers of people have acquired powerboats and plantings of salmonines have increased. ... The expansion of sport fisheries in the Great Lakes has placed new and increasing demands on managers to ensure good supplies of desirable fish species. Satisfaction among Lake Michigan anglers with the present, artificially maintained fishery for Pacific salmons has prompted managers in bordering states to consider maintenance of the status quo (the salmon–alewife system) as a primary management objective (Kitchell and Hewett 1987)."* (Loftus et al. 1987, p. 420)

and

> *"It is ironic that the species that was once considered a major pest is now the object of management concern for its protection as the forage base for the economically important Pacific salmonine fishery."* (Kocik and Jones 1999, p. 477)

and

> *"Initial [Great Lakes] management efforts focused on reducing the abundance of alewives, first by commercial harvest, and later, by stocking salmonines to eat them. Then, as a valuable sport fishery developed, managers focused on maintaining sufficient numbers to sustain the piscivores, and finally, as alewife numbers waned, management efforts turned to conserving the diminished populations to preserve the sort fishery."* (O'Gorman and Stewart 1999, p. 489)

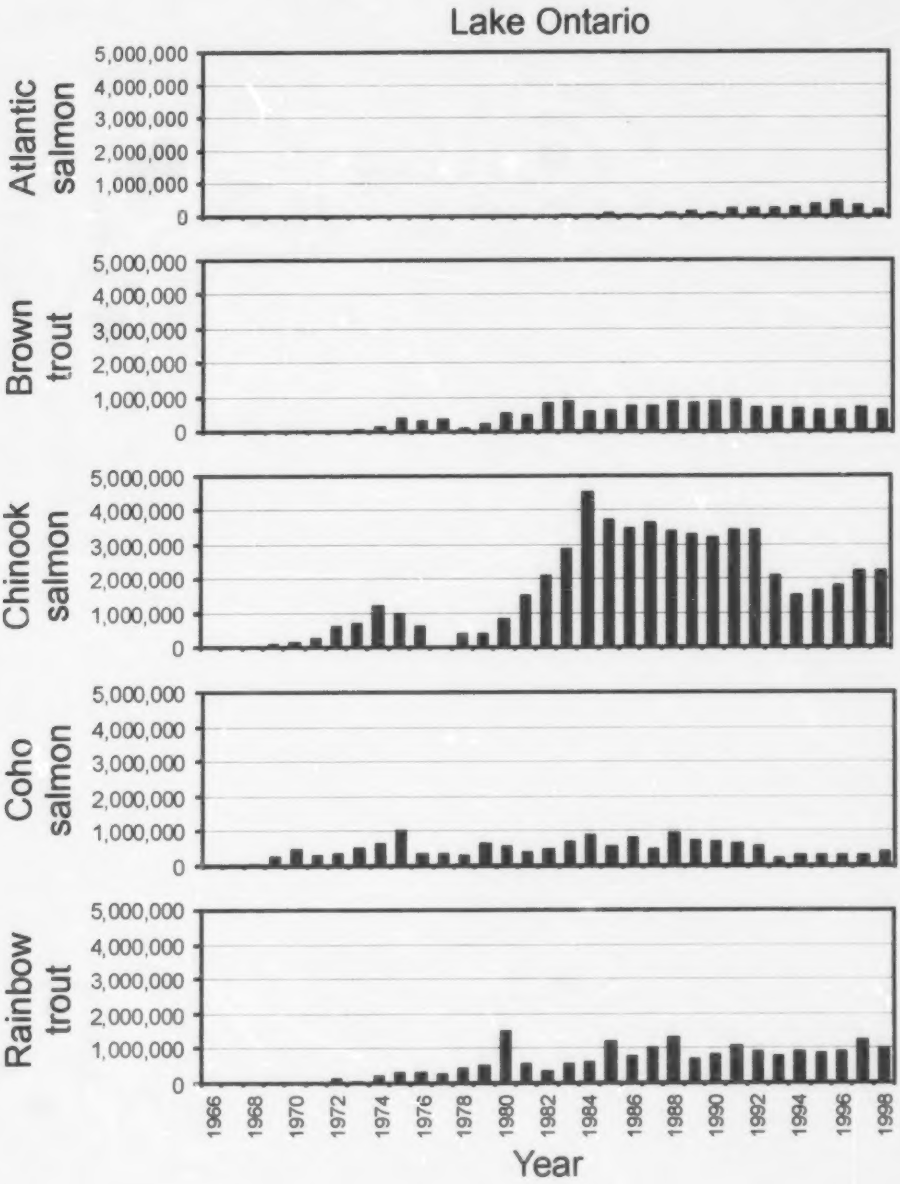
Thus, alewife have transformed from a novelty, to a nuisance, and finally to an important prey resource that must be carefully protected. Similar attitudes have been expressed regarding the forage value of rainbow smelt (e.g., Frie and Spangler 1985). Considering the available evidence, it should be apparent that the biological control programs described by some modern Great Lakes fisheries managers have more to do with "*red herrings*," than with alewife or rainbow smelt.

Why reduce stocking? "*Ultimately, to keep recreational fishery at a sustainable level*" (LHMU 1998, p. 71). Why try to keep the recreational salmon fishery going? Because "*the economics of Great Lakes fisheries favors anglers*" (Eshenroder and Burnham-Curtis 1999, p. 168). Follow the money and follow the votes; politicians give the people (or just the salmon fishermen?) what they want. When we remove biological control from the list of authentic objectives for Great Lakes salmonine introductions, we are left with only one primary objective — the development and maintenance of recreational salmon fisheries.

According to data available from the Great Lakes Fishery Commission and it's member agencies, more than 745 million introduced salmonines have been stocked into the Great Lakes ecosystem during the period 1966 to 1998 (Appendix I). This represents an average of more than 61,000 non-native fish, intentionally released to the ecosystem on each and every single day for 33 years. In contrast, a colleague of mine recently remarked on how good it felt for him to re-introduce a total of 65 Atlantic salmon to their native range in Wilmot's Creek.

In Lake Ontario, the stocking of non-native salmonines has been largely dominated by chinook salmon, with much smaller releases of coho salmon, brown trout and rainbow trout (Fig. 40 — note the contribution to Atlantic salmon reintroduction). In Lake Erie, chinook and coho salmon have trailed off to make way for increasing

Fig. 40. Number of non-native salmonines stocked by species in Lake Ontario for the period 1966–1998.



releases of rainbow trout (Fig. 41). Lake Huron stocking programs have focussed largely on chinook salmon, with a dramatic increase in stocking effort to reach a sustained plateau of approximately 4 million fish per year (Fig. 42). Lake Michigan stocking programs have been most diverse in introduced salmonine species, with stocking intensity ranked as follows: (1) chinook salmon, (2) coho salmon, (3) rainbow trout and (4) brown trout (Fig. 43). Lake Superior has been predominantly characterized by fairly intense and consistent releases of chinook salmon, and somewhat erratic pulses of rainbow trout stocking (Fig. 44)

Taken as a whole, the intentional introduction of non-native salmonines to the Great Lakes ecosystem can be summarized by Fig. 45 and Table 5. A total of more than 745 million fish, from 5 non-native species, released into 5 Great Lakes. It is interesting to note that 45% of all releases have taken place in Lake Michigan, and that 45% of all releases have been chinook salmon. American government and private hatcheries have been responsible for the vast majority of non-native salmonine stocking in the modern era; accounting for more than 91% of the total 745 million introduced fish released in the Great Lakes from 1966 to 1998 (Appendix I).

Keeping this stocking overview in mind, we may contrast non-native salmonine stocking effort with estimates of recreational fishing effort for those same Great Lakes. Table 6 shows estimates of 1990/91 recreational fishing effort in the Great Lakes by United States and Ontario residents (Bence and Smith 1999, p. 261). A couple of important observations can be made on the basis of these summary data. First, if the lakewide stocking of introduced salmonines was directly related to the recreational fishing effort for that lake, then Lake Erie would clearly be the most heavily stocked of all the Great Lakes. Ironically, the available evidence shows that Lake Erie is actually among the least stocked of the Great Lakes (Table 5). In fact, recreational fishermen on Lake Erie have shown that they prefer to satisfy their fishing desires with native species such as walleye, smallmouth bass, and yellow perch (OMNR 1998). Second, the intense stocking programs that fisheries managers have established on Lake Michigan are really quite out of proportion with the intensity of recreational fishing on that lake — more than 45% of all non-native salmonines stocked in the Great Lakes were released in Lake Michigan, despite the fact that it received only 17% of Great Lakes recreational fishing effort. This observation raises questions about the social and political factors that could force fisheries managers to heavily overstock these lakes with introduced salmonines, in order to support the demands of a particular component of the recreational fishery (i.e., salmon fishermen). Finally, from an international perspective, it would seem that the next major battle over introduced salmonines is likely to be on Lake Huron; a lake which already receives the second largest recreational fishing effort of the Great Lakes, and a lake which is currently experiencing a dramatic increase in growth rates of nearby human communities in both Michigan and Ontario (see Groop 1999, Fig. 3).

Where does this leave the native species of the Great Lakes, or the humans that may have an interest other than recreational salmon fishing? Take for example, the controversy that is currently brewing about management of Lake Michigan fisheries (see also Bence and Smith 1999):

Fig. 41. Number of non-native salmonines stocked by species in Lake Erie for the period 1966–1998.

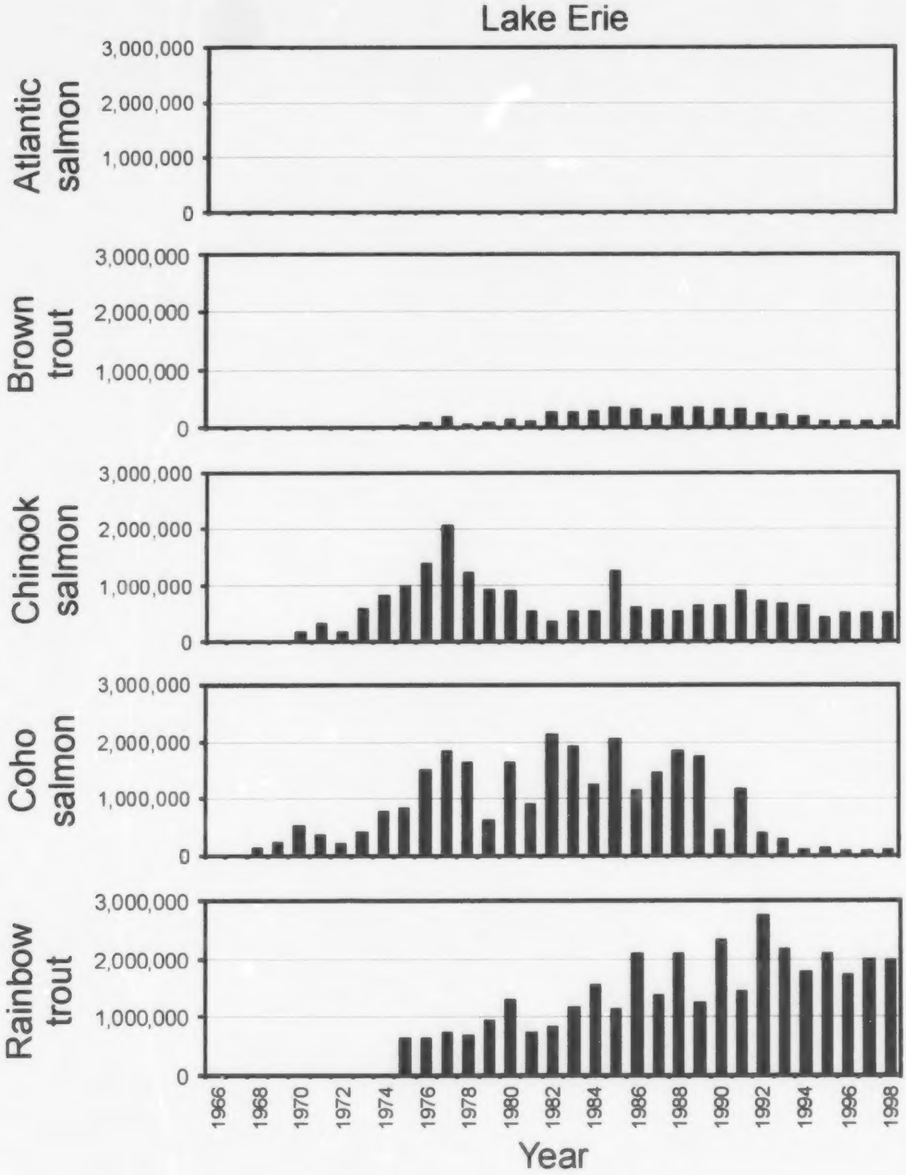


Fig. 42. Number of non-native salmonines stocked by species in Lake Huron for the period 1966–1998.

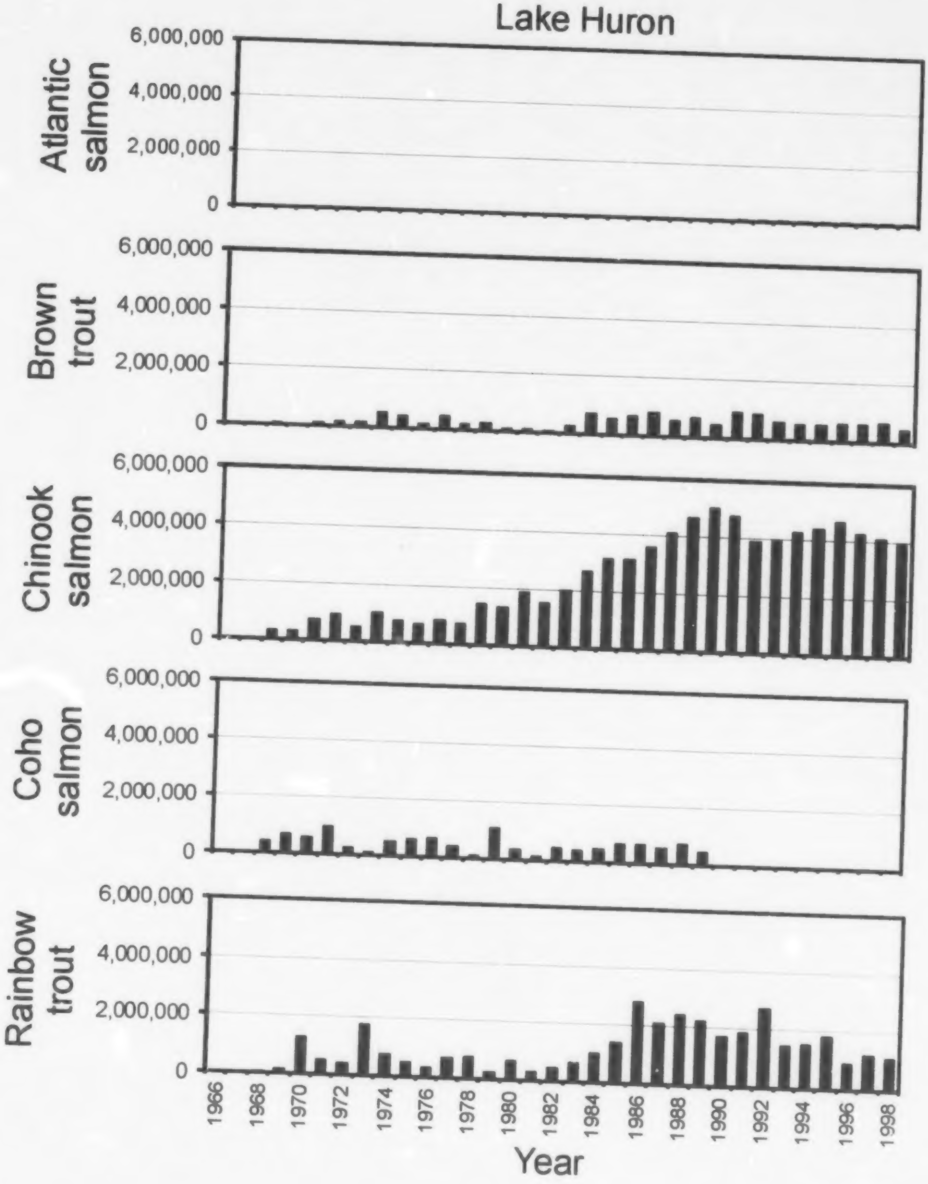


Fig. 43. Number of non-native salmonines stocked by species in Lake Michigan for the period 1966–1998.

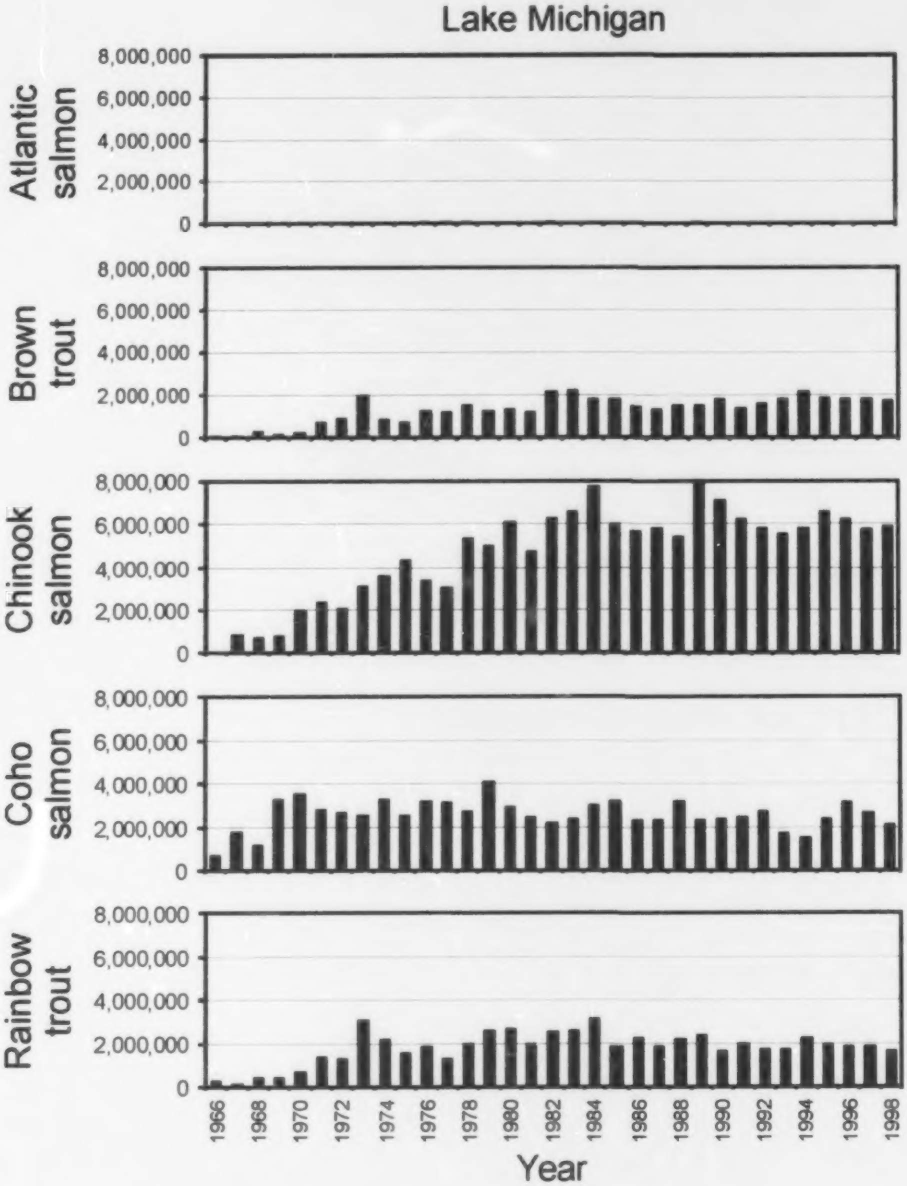


Fig. 44. Number of non-native salmonines stocked by species in Lake Superior for the period 1966–1998.

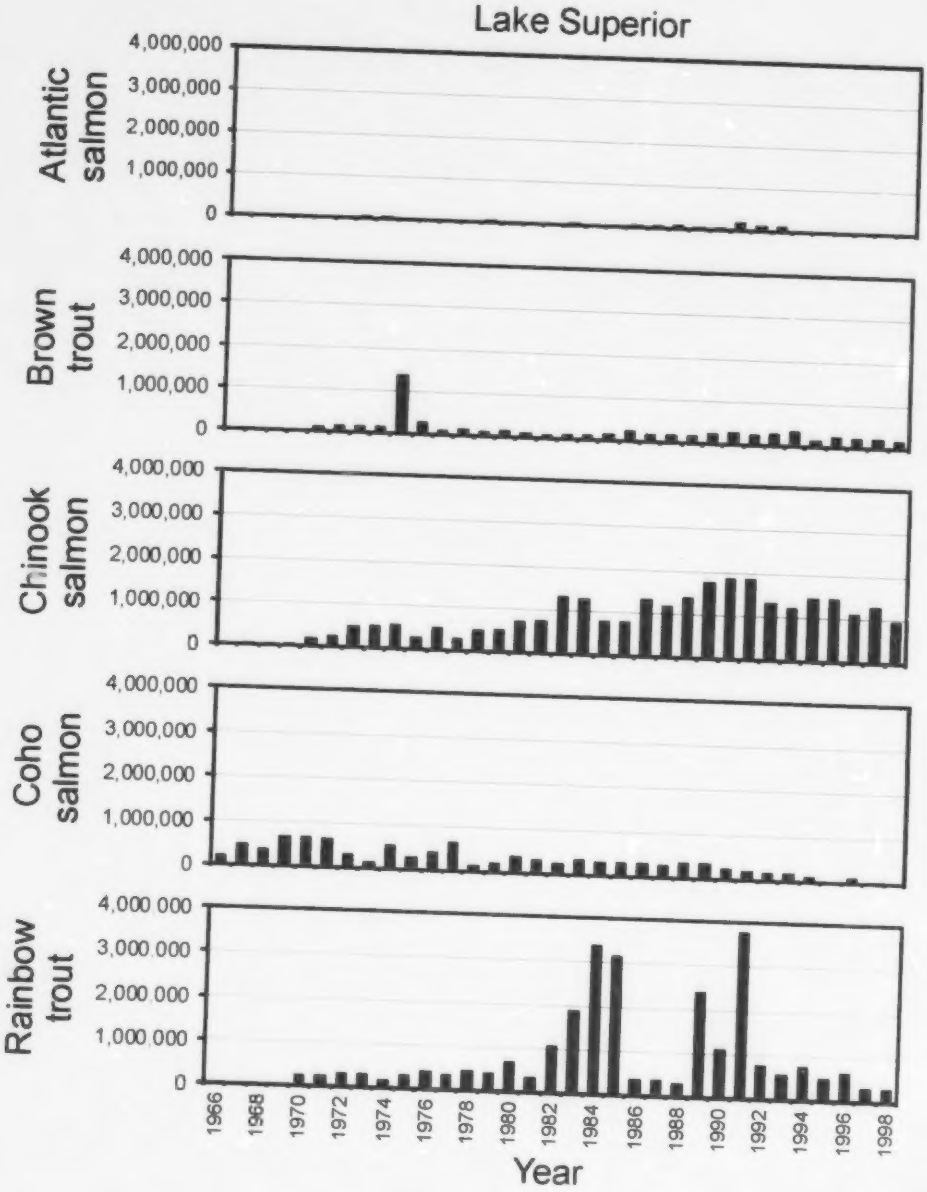


Fig. 45. Number of non-native salmonines stocked by species in the Laurentian Great Lakes for the period 1966–1998.

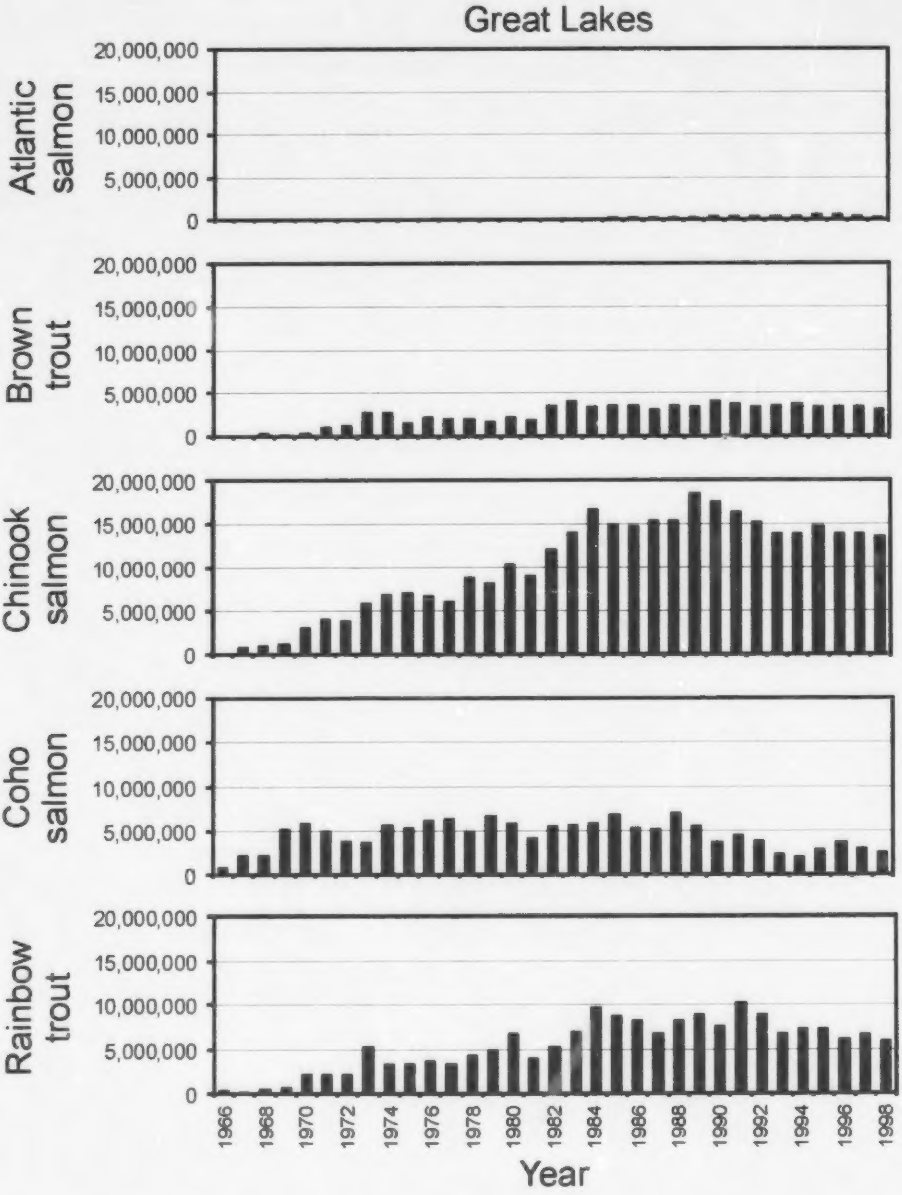


Table 5. Total number of introduced salmonines stocked in the Laurentian Great Lakes for the period 1966–1998, by species and by lake basin. Source: Great Lakes Fishery Commission stocking database (March 2000) with additional updates (Appendix 1).

	Lake basin						
Species	Ontario	Erie	Huron	Michigan	Superior	Great Lakes	%
Atlantic salmon	2,742,528	0	437,828	347,275	707,466	4,235,097	0.6
brown trout	14,660,241	4,582,746	13,031,054	42,995,500	6,265,892	81,535,433	10.9
chinook salmon	55,954,551	20,327,547	79,653,408	153,013,021	27,612,465	336,560,992	45.2
coho salmon	15,251,153	27,745,613	11,302,790	84,242,282	9,531,780	148,073,618	19.9
rainbow trout	19,177,898	35,329,766	35,888,897	58,674,554	25,647,791	174,718,906	23.4
Subtotal	107,786,371	87,985,672	140,313,977	339,272,632	69,765,394	745,124,046	
%	14.5	11.8	18.8	45.5	9.4		

Note: Atlantic salmon were native to the Lake Ontario drainage basin prior to their extinction circa 1900.

Table 6. Estimates of 1990/91 recreational fishing effort by water body/type within the Great Lakes by Ontario and United States residents based on federal mail and phone surveys. Source: Bence and Smith (1999, p. 261).

	Canadian recreational fishing[a]		U.S. recreational fishing		Total recreational fishing	
Water body	Days fishing (×1,000)	Percent of total	Days fishing (×1,000)	Percent of total	Days fishing (×1,000)	Percent of total
Lake Superior	352	3.4	883	4.6	1,235	4.2
Lake Michigan	0	0.0	5,090	26.5	5,090	17.3
Lake Huron	4,579	44.7	2,113	11.0	6,692	22.7
Lake Erie[b]	1,916	18.7	8,742	45.5	10,658	36.2
Lake Ontario	3,397	33.2	2,394	12.4	5,791	19.6
Great Lakes	10,244	100.0	19,222	100.0	29,466	100.0

[a] Data for national residents only.

[b] Includes data for Lake St. Clair.

> *"Fisheries managers and the general public need to recognize the potential conflict between conserving alewives for the Pacific salmonine forage base and achieving long-term sustainability of the yellow perch fishery. Stewart and Ibarra (1991) suggested fisheries managers might be able to "have their cake and eat it, too" by managing alewives at a level that provides adequate forage for Pacific salmonines yet still allows rehabilitation of indigenous fishes. Our results indicate the yellow perch fishery is unlikely to fully recover unless mean alewife abundance returns to an extremely low level, similar to that of the early to mid 1980s, when Pacific salmonines showed signs of inadequate forage (Stewart and Ibarra 1991). This suggests that fisheries managers must choose between conserving alewife stocks for the benefit of Pacific salmonines or trying to reduce alewife abundance so that yellow perch may again flourish. The second alternative, if successful, would probably result in decreased growth and condition of Pacific salmonines (Stewart and Ibarra 1991)."* (Shroyer and McComish 2000, p. 224)

Clearly, the managers of Great Lakes fisheries cannot "*have their cake and eat it too*" — the demands by recreational fisheries for introduced salmonines are simply inconsistent with the needs of the rest of the ecosystem. Something has to give.

General conclusions

The ongoing introduction of non-native salmonines continues to pose an ecologically significant risk to the Great Lakes ecosystem and its native community of organisms. The modern emphasis on introduced salmonines in the Great Lakes reflects a scientifically obsolete and dangerous philosophy of "*wise use*" that ignores the evolutionary and ecological relationships that exist within the native communities. Our 'modern' approach to developing and maintaining recreational fisheries with introduced salmonines has been driven mostly by political agendas which are neither ecologically nor scientifically based:

> *"Management is strongly influenced, however, by clients who demand Pacific salmon. The most challenging problems in moving the Great Lakes fish community to a more sustainable configuration are social as they are elsewhere (Ludwig et al. 1993). The Pacific salmon enhancement programs lack a strong ecological and ethical foundation (Eshenroder et al. 1995b). For example, substantial artificial propagation is necessary for their continuance, and the availability of introduced salmonines has resulted in a loss of respect for native species. Before any progress can be made in placing these programs on a stronger ecological footing, managers need to sort out their role in resource conservation, identify their clients beyond consumptive users, and establish the role of clients in policy development. Managers have a responsibility to sustain the resource, applying the best available science. The ecological framework for management is too often determined by resource users, and application of ecological principles and insights becomes restrained by social preference to a tiny range of options. This approach is not appropriate for systems over which humans have limited control."* (Eshenroder and Burnham-Curtis 1999, p. 174)

In the recent era, there really haven't been any valid excuses for failure to conduct the necessary ecological evaluations — especially when clear warnings were made on this issue during the early days (e.g., Regier 1968), and were repeated on numerous occasions in the scientific literature. It is clear from the available documentation that fisheries managers in the mid-1960s knew what they were not doing. To use Hoffmann's phrase, at least some people of the mid-1960s did indeed "*share the values of today's ecologists.*"

Given the astounding magnitude of Great Lakes salmonine introduction programs, it is inconceivable that no federal or state or provincial government agency attempted to:

(1) Evaluate the expected or observed ecological effects of introducing salmonines on Great Lakes ecosystems, or

(2) Determine, on the basis of such an ecological evaluation, whether to allow or prohibit the continued introduction of salmonines to the Great Lakes basin.

It is important to recognize that there is a burden of proof in this issue, and it has always rested with the proponent's ability to demonstrate the absence of significantly negative ecological effects resulting from salmonine introductions to the Great Lakes (FAO 1996, 1999). No such proof has ever been established by proponents of ongoing salmonine introductions to the Great Lakes. Either they really do believe that things couldn't possibly be worse, or they simply don't want to know about the ecological costs associated with their recreational activities.

Perhaps the most general conclusion that can be made from the available ecological evidence is this; despite the fanatical popularity of introduced salmonines among recreational fishermen and fisheries managers, these beasts are simply not well-adapted for life in the Great Lakes. This report has documented the futility of trying to force mismatched pieces into an ecological puzzle that defies control. Of course, these observations of ecological dysfunction should not come as a big surprise. By definition, the introduced salmonines evolved under ecological circumstances that differ from the Great Lakes ecosystem, both historical and contemporary (Teel et al. 2000). It would be unreasonable to expect that any introduced salmonine would somehow do a better job of truly complementing the structure and function of a wild ecosystem — no matter how disturbed — compared to the native species that evolved there.

What should the future hold for salmonine introductions to the Great Lakes? I will elaborate on this issue in a different forum — one which is more appropriate for dealing with controversial social, political and legal opinions. However, for the purposes of this scientific report, we can derive several general lessons from history that can be — and should be — applied in the future. First, we should be more forthright about what our fisheries objectives are for the Great Lakes; only when values and attitudes are face-up on the table can we begin reaching for consensus and making truly wise decisions. Second, we should shift from treating the symptoms of Great Lakes fisheries problems to dealing with the causes of those problems. Third, we should start making Great Lakes fisheries management decisions on the basis of ecological considerations, as well as satisfying social or economic objectives. Fourth, we should demand that Great Lakes fisheries management be based on valid scientific methods.

Finally, and most importantly for this report, we must recognize that the introduction of salmonines to the Great Lakes is — and always has been — a "*game of chance*" (Magnuson 1976). Based on consideration of all the information I was able to compile for this review, in the end I must agree with Krueger and May (1991) that this game should come to an end:

"Clearly, the era of widespread, intentional introductions of salmonids and other fish species as a fishery management activity justifiably is drawing to a close." (Krueger and May 1991, p. 74)

5

Epilogue: a policy of action

As described in this monograph, Dr. Howard Tanner was a principal motivating force behind the modern era of salmonine introductions to the Great Lakes. In a recent *Fisheries* journal supplement, entitled "*Celebrating 50 Years of the Sport Fish Restoration Program,*" Dr. Tanner provided a revealing reflection on non-native salmonine stocking in the Great Lakes:

> *"The changes necessary to restore the vitality of the Great Lakes fishery were at hand. It would take bold innovation and rebuilding almost from scratch. But the science and resources were on the threshold. Finding the dollars, will, and proper political climate to meld them together was the challenge. Experiments with chemical lamprey treatment succeeded and a new lake trout hatchery along the Jordan River could produce millions of young fish for restocking. However, a clash developed in the formative stage of implementing this strategy. Federal officials in the U.S. Bureau of Commercial Fisheries, based in Ann Arbor, Michigan, had—due to default on the part of the states—been managing the Great Lakes fisheries for decades. Under its jurisdiction, the resource was managed as a commercial fishery. These officials pressed to maintain their control. Their vision was to "turn back the clock," using native species exclusively, meaning lake trout. While Michigan fisheries officials sanctioned restoring lake trout, they had a broader vision, and for the first time since the turn of the century exerted their authority over the 41 percent of Great Lakes waters that were within the borders of the state of Michigan. These officials decided that management of Michigan's share of the Great Lakes for sport fishing was the best allocation of the resource. This decision has since been emulated to a substantial degree in the management policies of the other seven Great Lakes states and the province of Ontario. Because of these early decisions, sportfishing has become the key value for almost 100,000 square miles of productive freshwater."* (Tanner 2000, p. s13, his emphasis)

Clearly, from Tanner's retrospective, the intentional and ongoing introduction of non-native salmonines to the Great Lakes basin has been nothing short of a complete fisheries management triumph. Many fisheries managers and recreational fishermen would agree with this interpretation, and would strongly urge that the stocking programs be maintained.

To convey the opposite perspective, I return to 1968 and a landmark conference of fisheries scientists "*A Symposium on Introductions of Exotic Species*" held by the Ontario Department of Lands and Forests (Ken Loftus, convener). At this symposium, Prof. Henry Regier foreshadowed the ecological problems that could be expected as a consequence of the plans to introduce non-native salmonines to the Great Lakes ecosystem. From the beginning of my research on this issue, I have returned to Regier's warning time and again. Some readers will be upset with the manner that he refers to recreational anglers, fisheries managers, politicians and the public. However, my focus is on two important features. First, it clearly shows the foresight expressed by some ecologists about salmonine introductions to the Great Lakes. Second, and more important, it reminds us that actions speak louder than words.

> *"Basically most introductions of exotics have, I suggest, been part of a policy of retreat on the part of resource managers and politicians before man's thoughtless onslaught on the environment or before the sportsman's vibrant enthusiasms, or both.*
>
> *As ecologists we are embarrassingly ignorant of the proximate causes of the decline of valued fish stocks. We may not even yet have consensus that most of these declines are due to man's activities. Our ignorance is only partly due to our limited numbers and funds for research in comparison to the complexity of the problem. It is easier to measure fish, tabulate sex ratios, estimate growth by back-calculation, etc., than ask what really has caused the decline of one valued species after another.*
>
> *And now we appear to have entered another great era of introducing exotics. What has gone before seems to be unintelligible and at any rate irrelevant noise. Beginning now we will research the system so that if our introductions fail we will know why. I don't believe it! Aren't we really only trying anything that comes to mind? Put enough money into it and it will work. Our hatchery technology will get us a showing at any rate.*
>
> *Unlike the Foreign Game Introduction Program, recent attempts in the Great Lakes to introduce exotics are not all "a slow, careful searching for and evaluation of new species to supplement the old."*
>
> *Fishery biologists on the Great Lakes feel some responsibility for the mess that the system is in, and rightly so. However, the greatest blame goes elsewhere. It belongs to those who have fouled the waters, dammed the tributaries, and in one of a hundred ways destroyed the native communities. If one sought to identify who in society benefited most directly from such acts one might in fact find a considerable overlap with the more brassy, aggressive, demanding part of the angler brotherhood. I suggest that we try to identify whom we are seeking to please by providing 10-pound salmon or striped bass! If we find these are by and large uninhibited exploitive personalities, then I suggest we reflect on whether we really want to knock ourselves out to provide them with the sort of diversions they seek.*
>
> *I suggest we decide to stop retreating and that we start counter-attacking. Let's address ourselves explicitly to our society's ignorance (a less charitable term would be stupidity) as reflected in its destruction of the natural environment either by direct exploitation or by indirect means or both."* (Regier 1968, p. 106)

6

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APPENDIX I

Introduced salmonine stocking data summary for the Laurentian Great Lakes (1966–1998)

Compiled from various sources by Stephen Crawford (July 2000)

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Primary source

GLFC. 2000. Great Lakes Fishery Commission fish stocking database (1966–1998) received March 2000 from Mark Holey (U.S. Fish & Wildlife Service) via Stewart Cogswell.

Additional sources

LOMU. 1997. Lake Ontario fish stocking records (1968–1998) — unofficial. Compiled by Ontario Ministry of Natural Resources, Lake Ontario Management Unit. (received April 2000). 1998 updates from T. Stewart.

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LETC. 2000. GLFC Lake Erie Technical Committee database on fish stocking (1987–1998). Copy received 7 and 12 April 2000 from C. Murray.

LMTC. 2000. Lake Michigan stocking summary database (1976–1999). Copy received 20 April 2000 from M. Holey.

LSMU. 2000. Lake Superior fish stocking records for Ontario (1970–1999). Compiled by Ontario Ministry of Natural Resources, Lake Superior Management Unit. Copy received 29 June 2000 from M. Petzold.

LSTC. 2000. Lake Superior stocking summary database for U.S. States (1970–1999). Copy received 21 June 2000 from D. Schreiner.

Data notes

1. In many cases, information on developmental state at stocking was not available; therefore calculations were based on numbers stocked regardless of state.
2. Yearling equivalent conversions used by OMNR Lake Ontario and some Lake Erie reports as per Jones et al. (1993, table 2).
3. From the primary USFWS database all Canadian records (“OMNR” + “CFIP”) were pooled, and all U.S. records (i.e., all States) were pooled.
4. Lake Erie data include brown trout and rainbow trout stocked in Lake St. Clair.
5. Where stocking data from different sources conflicted in quantity, the larger of the two reported quantities was typically accepted.
6. Detailed copies of email communications and data file transfers from source agencies are available.

APPENDIX I

Salmonine stocking data summary for the Laurentian Great Lakes (1966–1998)

Appendix I*a*. Atlantic salmon (*Salmo salar*) stocking data summary for the Laurentian Great Lakes (1966–1998).

	Lake Ontario			Lake Erie			Lake Huron		
Year	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
1966	0	0	0	0	0	0	0	0	0
1967	0	0	0	0	0	0	0	0	0
1968	0	0	0	0	0	0	0	0	0
1969	0	0	0	0	0	0	0	0	0
1970	0	0	0	0	0	0	0	0	0
1971	0	0	0	0	0	0	0	0	0
1972	0	0	0	0	0	0	0	0	0
1973	0	0	0	0	0	0	0	0	0
1974	0	0	0	0	0	0	0	0	0
1975	0	0	0	0	0	0	0	0	0
1976	0	0	0	0	0	0	0	0	0
1977	0	0	0	0	0	0	0	0	0
1978	0	0	0	0	0	0	0	0	0
1979	0	0	0	0	0	0	0	0	0
1980	0	0	0	0	0	0	0	0	0
1981	0	0	0	0	0	0	0	0	0
1982	0	0	0	0	0	0	0	0	0
1983	49,000	0	49,000	0	0	0	0	0	0
1984	25,000	0	25,000	0	0	0	0	0	0
1985	68,000	0	68,000	0	0	0	0	0	0
1986	55,400	0	55,400	0	0	0	0	0	0
1987	65,329	1,009	66,338	0	0	0	0	0	0
1988	37,430	48,995	86,425	0	0	0	0	0	0
1989	65,000	76,000	141,000	0	0	0	18,596	0	18,596
1990	33,000	61,000	94,000	0	0	0	33,253	0	33,253
1991	178,000	28,000	206,000	0	0	0	32,804	0	32,804
1992	169,000	35,000	204,000	0	0	0	42,203	0	42,203
1993	165,500	57,000	222,500	0	0	0	70,164	0	70,164
1994	189,000	67,000	256,000	0	0	0	33,275	0	33,275
1995	226,150	135,000	361,150	0	0	0	68,066	0	68,066
1996	304,000	130,628	434,628	0	0	0	43,725	0	43,725
1997	175,000	138,087	313,087	0	0	0	43,568	0	43,568
1998	102,000	58,000	160,000	0	0	0	52,174	0	52,174
Subtotal	1,906,809	835,719	2,742,528	0	0	0	437,828	0	437,828

Appendix I*b*. Brown trout (*Salmo trutta*) stocking data summary for the Laurentian Great Lakes (1966–1998).

	Lake Ontario			Lake Erie			Lake Huron		
Year	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
1966	0	0	0	0	0	0	0	0	0
1967	0	0	0	0	0	0	0	0	0
1968	0	0	0	0	0	0	45,000	0	45,000
1969	0	0	0	0	0	0	0	0	0
1970	0	0	0	0	0	0	81,870	0	81,870
1971	0	0	0	0	0	0	159,291	0	159,291
1972	0	0	0	0	0	0	160,000	0	160,000
1973	60,000	0	60,000	0	0	0	496,552	0	496,552
1974	123,000	0	123,000	0	0	0	420,109	0	420,109
1975	370,700	0	370,700	33,230	0	33,230	155,025	0	155,025
1976	310,751	0	310,751	78,232	0	78,232	446,842	0	446,842
1977	358,000	0	358,000	173,695	0	173,695	210,014	0	210,014
1978	93,542	0	93,542	61,890	0	61,890	258,232	0	258,232
1979	218,690	0	218,690	76,990	0	76,990	98,000	0	98,000
1980	528,780	0	528,780	127,643	0	127,643	90,000	0	90,000
1981	453,800	7,000	460,800	110,656	0	110,656	45,000	0	45,000
1982	753,960	57,150	811,110	217,273	47,500	264,773	250,000	0	250,000
1983	711,600	123,300	834,900	182,006	69,000	251,006	689,287	8,190	697,477
1984	407,650	165,822	573,472	241,836	47,200	289,036	555,520	10,000	565,520
1985	439,920	163,854	603,774	252,857	70,639	323,496	623,067	10,224	633,291
1986	442,320	297,872	740,192	199,091	99,300	298,391	766,563	61,609	828,172
1987	417,760	318,903	736,663	126,908	84,500	211,408	488,527	59,491	548,018
1988	450,680	387,806	838,486	264,011	70,114	334,125	528,126	108,976	637,102
1989	445,000	360,000	805,000	259,510	70,530	330,040	395,068	80,000	475,068
1990	461,000	387,000	848,000	214,200	89,993	304,193	706,449	180,000	886,449
1991	382,000	526,000	908,000	220,500	84,948	305,448	648,632	197,262	845,894
1992	415,000	257,000	672,000	158,270	68,300	226,570	430,373	150,000	580,373
1993	445,000	219,000	664,000	124,321	84,802	209,123	420,594	110,000	530,594
1994	402,000	235,000	637,000	112,464	70,963	183,427	349,587	208,232	557,819
1995	381,570	203,000	584,570	30,350	64,950	95,300	325,454	304,577	630,031
1996	361,250	255,757	617,007	38,850	65,349	104,199	295,540	299,357	594,897
1997	425,750	246,054	671,804	31,845	65,000	96,845	408,405	230,000	638,405
1998	426,000	164,000	590,000	28,030	65,000	93,030	341,884	124,125	466,009
Subtotal	10,285,723	4,374,518	14,660,241	3,364,658	1,218,088	4,582,746	10,889,011	2,142,043	13,031,054

Appendix I*a* (*concluded*).

Lake Michigan			Lake Superior			Great Lakes (combined)		
U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
0	n/a	0	0	0	0	0	0	0
0	n/a	0	0	0	0	0	0	0
0	n/a	0	0	0	0	0	0	0
0	n/a	0	0	0	0	0	0	0
0	n/a	0	0	0	0	0	0	0
0	n/a	0	0	0	0	0	0	0
10,000	n/a	10,000	20,000	0	20,000	30,000	0	30,000
15,000	n/a	15,000	20,000	0	20,000	35,000	0	35,000
21,863	n/a	21,863	0	0	0	21,863	0	21,863
22,172	n/a	22,172	0	0	0	22,172	0	22,172
43,000	n/a	43,000	9,100	0	9,100	52,100	0	52,100
47,000	n/a	47,000	200	0	200	47,200	0	47,200
46,212	n/a	46,212	37,000	0	37,000	83,212	0	83,212
0	n/a	0	0	0	0	0	0	0
0	n/a	0	0	0	0	0	0	0
19,558	n/a	19,558	0	0	0	19,558	0	19,558
45,030	n/a	45,030	17,952	0	17,952	62,982	0	62,982
0	n/a	0	11,025	0	11,025	60,025	0	60,025
0	n/a	0	11,866	0	11,866	36,866	0	36,866
0	n/a	0	25,154	0	25,154	93,154	0	93,154
0	n/a	0	42,041	0	42,041	97,441	0	97,441
0	n/a	0	72,258	0	72,258	137,587	1,009	138,596
17,340	n/a	17,340	49,093	0	49,093	103,863	48,995	152,858
60,100	n/a	60,100	31,251	0	31,251	174,947	76,000	250,947
0	n/a	0	173,702	0	173,702	239,955	61,000	300,955
0	n/a	0	88,576	0	88,576	299,380	28,000	327,380
0	n/a	0	98,248	0	98,248	309,451	35,000	344,451
0	n/a	0	0	0	0	235,664	57,000	292,664
0	n/a	0	0	0	0	222,275	67,000	289,275
0	n/a	0	0	0	0	294,216	135,000	429,216
0	n/a	0	0	0	0	347,725	130,628	478,353
0	n/a	0	0	0	0	218,568	138,087	356,655
0	n/a	0	0	0	0	154,174	58,000	212,174
347,275	n/a	347,275	707,466	0	707,466	3,399,378	835,719	4,235,097

Appendix I*b* (*concluded*).

Year	Lake Michigan			Lake Superior			Great Lakes (combined)		
	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
1966	38,000	n/a	38,000	0	0	0	38,000	0	38,000
1967	48,475	n/a	48,475	0	0	0	48,475	0	48,475
1968	251,590	n/a	251,590	0	0	0	296,590	0	296,590
1969	141,577	n/a	141,577	0	0	0	141,577	0	141,577
1970	224,360	n/a	224,360	104,300	0	104,300	410,530	0	410,530
1971	709,115	n/a	709,115	140,000	0	140,000	1,008,406	0	1,008,406
1972	926,209	n/a	926,209	144,500	0	144,500	1,230,709	0	1,230,709
1973	1,912,795	n/a	1,912,795	147,000	0	147,000	2,616,347	0	2,616,347
1974	832,658	n/a	832,658	1,373,000	0	1,373,000	2,748,767	0	2,748,767
1975	665,813	n/a	665,813	276,500	0	276,500	1,501,268	0	1,501,268
1976	1,257,810	n/a	1,257,810	112,500	0	112,500	2,206,135	0	2,206,135
1977	1,159,863	n/a	1,159,863	133,345	0	133,345	2,034,917	0	2,034,917
1978	1,502,529	n/a	1,502,529	111,100	0	111,100	2,027,293	0	2,027,293
1979	1,227,849	n/a	1,227,849	131,044	0	131,044	1,752,573	0	1,752,573
1980	1,291,838	n/a	1,291,838	93,000	0	93,000	2,131,261	0	2,131,261
1981	1,169,388	n/a	1,169,388	83,150	0	83,150	1,861,994	7,000	1,868,994
1982	2,138,993	n/a	2,138,993	102,475	0	102,475	3,462,701	104,650	3,567,351
1983	2,179,749	n/a	2,179,749	118,447	0	118,447	3,881,089	200,490	4,081,579
1984	1,802,946	n/a	1,802,946	153,638	0	153,638	3,161,590	223,022	3,384,612
1985	1,797,647	n/a	1,797,647	229,425	0	229,425	3,342,916	244,717	3,587,633
1986	1,434,053	n/a	1,434,053	168,770	0	168,770	3,010,797	458,781	3,469,578
1987	1,342,369	n/a	1,342,369	161,420	0	161,420	2,536,984	462,894	2,999,878
1988	1,515,735	n/a	1,515,735	159,510	0	159,510	2,918,062	566,896	3,484,958
1989	1,504,315	n/a	1,504,315	247,855	0	247,855	2,851,748	510,530	3,362,278
1990	1,771,701	n/a	1,771,701	264,545	0	264,545	3,417,895	656,993	4,074,888
1991	1,383,279	n/a	1,383,279	230,683	0	230,683	2,865,094	808,210	3,673,304
1992	1,614,607	n/a	1,614,607	285,900	0	285,900	2,904,150	475,300	3,379,450
1993	1,758,722	n/a	1,758,722	336,140	0	336,140	3,084,777	413,802	3,498,579
1994	2,172,380	n/a	2,172,380	149,600	0	149,600	3,186,031	514,195	3,700,226
1995	1,876,060	n/a	1,876,060	237,400	0	237,400	2,850,834	572,527	3,423,361
1996	1,786,746	n/a	1,786,746	197,635	0	197,635	2,680,021	620,463	3,300,484
1997	1,804,329	n/a	1,804,329	203,055	0	203,055	2,873,384	541,054	3,414,438
1998	1,752,000	n/a	1,752,000	169,955	0	169,955	2,717,869	353,125	3,070,994
Subtotal	42,995,500	n/a	42,995,500	6,265,892	0	6,265,892	73,800,784	7,734,649	81,535,433

Appendix Ic. Chinook salmon (*Oncorhynchus tshawytscha*) stocking data summary for the Laurentian Great Lakes (1966–1998).

	Lake Ontario			Lake Erie			Lake Huron		
Year	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
1966	0	0	0	0	0	0	0	0	0
1967	0	0	0	0	0	0	0	0	0
1968	0	0	0	0	0	0	300,000	0	300,000
1969	70,000	0	70,000	0	0	0	300,000	0	300,000
1970	141,000	0	141,000	150,000	0	150,000	700,000	0	700,000
1971	149,000	89,000	238,000	309,000	0	309,000	894,000	0	894,000
1972	425,800	189,860	615,660	150,000	0	150,000	514,545	0	514,545
1973	697,000	0	697,000	584,500	0	584,500	1,000,000	0	1,000,000
1974	963,300	224,550	1,187,850	815,804	0	815,804	776,294	0	776,294
1975	919,800	0	919,800	969,096	0	969,096	655,484	0	655,484
1976	593,400	0	593,400	1,380,782	0	1,380,782	830,536	0	830,536
1977	0	0	0	2,071,663	0	2,071,663	733,430	0	733,430
1978	0	392,608	392,608	1,237,783	0	1,237,783	1,417,578	0	1,417,578
1979	221,650	147,450	369,100	917,650	0	917,650	1,325,033	0	1,325,033
1980	788,070	18,000	806,070	893,722	0	893,722	1,877,645	0	1,877,645
1981	1,468,240	11,997	1,480,237	519,344	0	519,344	1,522,745	0	1,522,745
1982	1,808,000	269,886	2,077,886	326,660	0	326,660	2,000,787	0	2,000,787
1983	2,758,500	124,581	2,883,081	534,000	0	534,000	2,695,800	0	2,695,800
1984	3,878,300	662,400	4,540,700	533,343	0	533,343	3,146,997	0	3,146,997
1985	3,022,400	703,383	3,725,783	1,259,340	0	1,259,340	2,968,315	172,577	3,140,892
1986	2,849,200	597,542	3,446,742	592,600	0	592,600	3,285,122	324,130	3,609,252
1987	3,111,330	513,931	3,625,261	552,000	0	552,000	3,414,965	728,769	4,143,734
1988	2,868,000	516,000	3,384,000	520,000	0	520,000	3,520,429	1,172,898	4,693,327
1989	2,752,000	541,000	3,293,000	620,000	0	620,000	4,200,177	817,571	5,017,748
1990	2,720,000	497,000	3,217,000	624,200	0	624,200	3,834,970	932,961	4,767,931
1991	2,835,000	594,000	3,429,000	875,000	0	875,000	3,221,778	676,136	3,897,914
1992	2,798,000	605,000	3,403,000	697,000	0	697,000	3,047,701	928,151	3,975,852
1993	1,603,000	501,000	2,104,000	654,060	0	654,060	3,287,234	994,574	4,281,808
1994	1,000,000	475,000	1,475,000	620,000	0	620,000	3,572,559	845,398	4,417,957
1995	1,150,000	462,000	1,612,000	420,000	0	420,000	3,829,157	848,970	4,678,127
1996	1,359,200	438,073	1,797,273	500,000	0	500,000	3,471,523	780,646	4,252,169
1997	1,604,980	612,120	2,217,100	500,000	0	500,000	3,287,581	808,163	4,095,744
1998	1,596,000	617,000	2,213,000	500,000	0	500,000	3,311,052	679,027	3,990,079
Subtotal	46,151,170	9,803,381	55,954,551	20,327,547	0	20,327,547	68,943,437	10,709,971	79,653,408

Appendix Ic (*concluded*).

Year	Lake Michigan			Lake Superior			Great Lakes (combined)		
	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
1966	0	n/a	0	0	0	0	0	0	0
1967	801,390	n/a	801,390	33,460	0	33,460	834,850	0	834,850
1968	687,000	n/a	687,000	50,000	0	50,000	1,037,000	0	1,037,000
1969	718,000	n/a	718,000	50,000	0	50,000	1,138,000	0	1,138,000
1970	1,904,000	n/a	1,904,000	175,000	0	175,000	3,070,000	0	3,070,000
1971	2,317,000	n/a	2,317,000	252,000	0	252,000	3,921,000	89,000	4,010,000
1972	2,023,128	n/a	2,023,128	471,688	0	471,688	3,585,161	189,860	3,775,021
1973	3,045,767	n/a	3,045,767	508,647	0	508,647	5,835,914	0	5,835,914
1974	3,578,053	n/a	3,578,053	522,992	0	522,992	6,656,443	224,550	6,880,993
1975	4,279,782	n/a	4,279,782	252,762	0	252,762	7,076,924	0	7,076,924
1976	3,317,057	n/a	3,317,057	492,519	0	492,519	6,614,294	0	6,614,294
1977	2,976,879	n/a	2,976,879	253,495	0	253,495	6,035,467	0	6,035,467
1978	5,365,263	n/a	5,365,263	477,854	0	477,854	8,498,478	392,608	8,891,086
1979	4,984,271	n/a	4,984,271	500,574	0	500,574	7,949,178	147,450	8,096,628
1980	6,105,924	n/a	6,105,924	702,512	0	702,512	10,367,873	18,000	10,385,873
1981	4,746,993	n/a	4,746,993	728,088	0	728,088	8,985,410	11,997	8,997,407
1982	6,312,127	n/a	6,312,127	1,313,081	0	1,313,081	11,760,655	269,886	12,030,541
1983	6,539,413	n/a	6,539,413	1,277,264	0	1,277,264	13,804,977	124,581	13,929,558
1984	7,709,749	n/a	7,709,749	787,124	0	787,124	16,055,513	662,400	16,717,913
1985	5,956,023	n/a	5,956,023	764,884	0	764,884	13,970,962	875,960	14,846,922
1986	5,692,678	n/a	5,692,678	1,309,536	0	1,309,53	13,729,136	921,672	14,650,808
1987	5,800,757	n/a	5,800,757	1,193,272	0	1,193,272	14,072,324	1,242,700	15,315,024
1988	5,416,870	n/a	5,416,870	1,155,135	225,939	1,381,074	13,480,434	1,914,837	15,395,271
1989	7,859,479	n/a	7,859,479	1,284,319	446,934	1,731,253	16,715,975	1,805,505	18,521,480
1990	7,128,723	n/a	7,128,723	1,234,049	608,653	1,842,702	15,541,942	2,038,614	17,580,556
1991	6,237,562	n/a	6,237,562	1,190,073	664,599	1,854,672	14,359,413	1,934,735	16,294,148
1992	5,795,465	n/a	5,795,465	561,953	733,166	1,295,119	12,900,119	2,266,317	15,166,436
1993	5,529,950	n/a	5,529,950	824,899	391,005	1,215,904	11,899,143	1,886,579	13,785,722
1994	5,836,855	n/a	5,836,855	957,955	484,111	1,442,066	11,987,369	1,804,509	13,791,878
1995	6,548,593	n/a	6,548,593	945,858	493,746	1,439,604	12,893,608	1,804,716	14,698,324
1996	6,193,377	n/a	6,193,377	875,528	227,819	1,103,347	12,399,628	1,446,538	13,846,166
1997	5,744,893	n/a	5,744,893	812,935	450,000	1,262,935	11,950,389	1,870,283	13,820,672
1998	5,860,000	n/a	5,860,000	627,037	300,000	927,037	11,894,089	1,596,027	13,490,116
Subtotal	153,013,021	n/a	153,013,021	22,586,493	5,025,972	27,612,465	311,021,668	25,539,324	336,560,992

Appendix Id. Coho salmon (*Oncorhynchus kisutch*) stocking data summary for the Laurentian Great Lakes (1966–1998).

	Lake Ontario			Lake Erie			Lake Huron		
Year	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
1966	0	0	0	0	0	0	0	0	0
1967	0	0	0	0	0	0	0	0	0
1968	40,000	0	40,000	121,000	0	121,000	402,000	0	402,000
1969	119,000	130,000	249,000	235,000	0	235,000	667,000	0	667,000
1970	300,000	145,000	445,000	515,000	0	515,000	571,000	0	571,000
1971	122,000	160,000	282,000	369,000	0	369,000	975,000	0	975,000
1972	230,100	121,500	351,600	218,428	0	218,428	249,046	0	249,046
1973	239,800	271,600	511,400	411,672	0	411,672	100,026	0	100,026
1974	216,800	438,425	655,225	783,326	0	783,326	500,048	0	500,048
1975	812,300	225,769	1,038,069	819,211	0	819,211	627,362	0	627,362
1976	177,575	165,855	343,430	1,490,656	0	1,490,656	690,529	0	690,529
1977	38,640	312,901	351,541	1,832,653	0	1,832,653	415,568	0	415,568
1978	79,937	201,073	281,010	1,631,219	0	1,631,219	84,176	0	84,176
1979	343,537	285,972	629,509	620,859	0	620,859	1,082,216	0	1,082,216
1980	299,000	249,000	548,000	1,621,114	0	1,621,114	375,130	0	375,130
1981	0	363,052	363,052	910,909	0	910,909	135,132	0	135,132
1982	367,400	112,033	479,433	2,116,316	0	2,116,316	452,589	0	452,589
1983	446,700	217,708	664,408	1,901,601	0	1,901,601	425,138	0	425,138
1984	742,550	131,128	873,678	1,243,942	0	1,243,942	470,051	0	470,051
1985	376,180	190,592	566,772	2,034,281	0	2,034,281	671,733	0	671,733
1986	547,500	272,957	820,457	1,139,003	0	1,139,003	675,259	0	675,259
1987	80,000	400,255	480,255	1,457,635	0	1,457,635	581,649	0	581,649
1988	556,250	386,878	943,128	1,832,232	0	1,832,232	702,034	0	702,034
1989	410,000	291,000	701,000	1,720,880	0	1,720,880	450,104	0	450,104
1990	441,000	235,000	676,000	434,540	0	434,540	0	0	0
1991	229,000	427,000	656,000	1,152,250	0	1,152,250	0	0	0
1992	539,000	0	539,000	375,750	0	375,750	0	0	0
1993	196,000	0	196,000	271,700	0	271,700	0	0	0
1994	315,000	0	315,000	112,900	0	112,900	0	0	0
1995	291,000	0	291,000	119,000	0	119,000	0	0	0
1996	294,000	0	294,000	72,000	0	72,000	0	0	0
1997	250,000	36,186	286,186	68,061	0	68,061	0	0	0
1998	245,000	135,000	380,000	113,475	0	113,475	0	0	0
Subtotal	9,345,269	5,905,884	15,251,153	27,745,613	0	27,745,613	11,302,790	0	11,302,790

Appendix I*d* (*concluded*).

Year	Lake Michigan			Lake Superior			Great Lakes (combined)		
	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
1966	659,400	n/a	659,400	192,400	0	192,400	851,800	0	851,800
1967	1,732,300	n/a	1,732,300	467,000	0	467,000	2,199,300	0	2,199,300
1968	1,176,000	n/a	1,176,000	374,000	0	374,000	2,113,000	0	2,113,000
1969	3,281,000	n/a	3,281,000	636,000	20,000	656,000	4,938,000	150,000	5,088,000
1970	3,553,000	n/a	3,553,000	618,000	31,000	649,000	5,557,000	176,000	5,733,000
1971	2,750,000	n/a	2,750,000	590,000	27,000	617,000	4,806,000	187,000	4,993,000
1972	2,619,506	n/a	2,619,506	296,604	0	296,604	3,613,684	121,500	3,735,184
1973	2,508,957	n/a	2,508,957	135,063	0	135,063	3,395,518	271,600	3,667,118
1974	3,230,972	n/a	3,230,972	529,243	0	529,243	5,260,389	438,425	5,698,814
1975	2,504,891	n/a	2,504,891	275,000	0	275,000	5,038,764	225,769	5,264,533
1976	3,196,399	n/a	3,196,399	400,000	0	400,000	5,955,159	165,855	6,121,014
1977	3,087,218	n/a	3,087,218	627,000	0	627,000	6,001,079	312,901	6,313,980
1978	2,685,041	n/a	2,685,041	140,245	0	140,245	4,620,618	201,073	4,821,691
1979	4,043,843	n/a	4,043,843	200,000	0	200,000	6,290,455	285,972	6,576,427
1980	2,943,370	n/a	2,943,370	350,273	0	350,273	5,588,887	249,000	5,837,887
1981	2,451,431	n/a	2,451,431	288,000	0	288,000	3,785,472	363,052	4,148,524
1982	2,180,531	n/a	2,180,531	235,644	2,090	237,734	5,352,480	114,123	5,466,603
1983	2,364,012	n/a	2,364,012	325,197	0	325,197	5,462,648	217,708	5,680,356
1984	2,954,047	n/a	2,954,047	299,874	0	299,874	5,710,464	131,128	5,841,592
1985	3,180,794	n/a	3,180,794	301,900	0	301,900	6,564,888	190,592	6,755,480
1986	2,291,397	n/a	2,291,397	287,511	0	287,511	4,940,670	272,957	5,213,627
1987	2,304,571	n/a	2,304,571	274,481	0	274,481	4,698,336	400,255	5,098,591
1988	3,210,093	n/a	3,210,093	334,163	0	334,163	6,634,772	386,878	7,021,650
1989	2,333,925	n/a	2,333,925	325,070	0	325,070	5,239,979	291,000	5,530,979
1990	2,380,053	n/a	2,380,053	220,248	0	220,248	3,475,841	235,000	3,710,841
1991	2,470,911	n/a	2,470,911	195,301	0	195,301	4,047,462	427,000	4,474,462
1992	2,742,210	n/a	2,742,210	178,114	0	178,114	3,835,074	0	3,835,074
1993	1,708,751	n/a	1,708,751	179,959	0	179,959	2,356,410	0	2,356,410
1994	1,496,564	n/a	1,496,564	87,700	0	87,700	2,012,164	0	2,012,164
1995	2,401,128	n/a	2,401,128	0	0	0	2,811,128	0	2,811,128
1996	3,111,931	n/a	3,111,931	87,700	0	87,700	3,565,631	0	3,565,631
1997	2,620,036	n/a	2,620,036	0	0	0	2,938,097	36,186	2,974,283
1998	2,068,000	n/a	2,068,000	0	0	0	2,426,475	135,000	2,561,475
Subtotal	84,242,282	n/a	84,242,282	9,451,690	80,090	9,531,780	142,08 7,644	5,985,974	148,073,618

Appendix I*e*. Rainbow trout (*Oncorhynchus mykiss*) stocking data summary for the Laurentian Great Lakes (1966–1998).

	Lake Ontario			Lake Erie			Lake Huron		
Year	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
1966	0	0	0	0	0	0	0	0	0
1967	0	0	0	0	0	0	0	0	0
1968	0	12,000	12,000	0	0	0	70,000	0	70,000
1969	0	10,000	10,000	0	0	0	151,020	0	151,020
1970	0	10,000	10,000	0	0	0	1,280,666	0	1,280,666
1971	0	18,000	18,000	0	0	0	507,022	0	507,022
1972	0	107,000	107,000	0	0	0	378,877	0	378,877
1973	0	58,000	58,000	0	0	0	1,779,304	0	1,779,304
1974	79,000	124,000	203,000	0	0	0	770,840	0	770,840
1975	251,700	29,468	281,168	306,692	323,020	629,712	446,615	62,000	508,615
1976	186,388	108,471	294,859	386,791	249,890	636,681	332,814	33,200	366,014
1977	151,529	109,710	261,239	449,878	287,414	737,292	167,517	544,408	711,925
1978	313,360	124,000	437,360	305,784	386,900	692,684	3 88,900	348,458	737,358
1979	24,960	201,000	525,960	570,574	365,550	936,124	200,000	46,700	246,700
1980	759,398	733,746	1,493,144	854,209	432,500	1,286,709	312,802	320,111	632,913
1981	482,830	81,234	564,064	722,322	12,081	734,403	211,243	82,200	293,443
1982	276,240	68,466	344,706	817,064	22,900	839,964	368,381	75,000	443,381
1983	464,473	104,915	569,388	1,139,990	12,000	1,151,990	420,000	230,000	650,000
1984	500,775	110,000	610,775	1,535,647	12,861	1,548,508	527,128	500,000	1,027,128
1985	1,081,512	106,231	1,187,743	1,119,888	23,582	1,143,470	1,100,559	330,000	1,430,559
1986	564,500	200,000	764,500	2,028,895	60,931	2,089,826	2,060,000	749,080	2,809,080
1987	703,490	307,260	1,010,750	1,362,492	8,275	1,370,767	1,399,153	710,000	2,109,153
1988	943,400	375,104	1,318,504	1,441,422	643,127	2,084,549	1,317,875	1,087,360	2,405,235
1989	578,000	118,000	696,000	1,226,921	14,370	1,241,291	1,130,000	1,080,000	2,210,000
1990	720,000	105,000	825,000	2,288,315	31,530	2,319,845	1,044,137	690,000	1,734,137
1991	877,000	187,000	1,064,000	1,332,009	98,200	1,430,209	1,150,000	723,524	1,873,524
1992	600,000	290,000	890,000	2,604,273	154,000	2,758,273	1,630,000	1,070,000	2,700,000
1993	542,000	216,000	758,000	2,137,199	24,177	2,161,376	576,652	910,000	1,486,652
1994	579,000	329,000	908,000	1,682,680	82,175	1,764,855	575,695	940,000	1,515,695
1995	609,020	240,000	849,020	2,031,909	60,410	2,092,319	624,996	1,210,000	1,834,996
1996	673,000	215,894	888,894	1,675,200	48,425	1,723,625	560,739	370,000	930,739
1997	757,920	489,904	1,247,824	1,945,055	51,565	1,996,620	600,072	600,000	1,200,072
1998	634,000	335,000	969,000	1,897,674	61,000	1,958,674	634,254	459,595	1,093,849
Subtotal	13,653,495	5,524,403	19,177,898	31,862,883	3,466,883	35,329,766	22,717,261	13,171,636	35,888,897

Appendix I*e* (*concluded*).

Year	Lake Michigan			Lake Superior			Great Lakes (combined)		
	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal	U.S.A.	Canada	Subtotal
1966	275,589	n/a	275,589	0	0	0	275,589	0	275,589
1967	116,860	n/a	116,860	0	0	0	116,860	0	116,860
1968	399,349	n/a	399,349	0	0	0	469,349	12,000	481,349
1969	431,654	n/a	431,654	0	0	0	582,674	10,000	592,674
1970	656,277	n/a	656,277	226,825	0	226,825	2,163,768	10,000	2,173,768
1971	1,368,428	n/a	1,368,428	238,600	0	238,600	2,114,050	18,000	2,132,050
1972	1,316,052	n/a	1,316,052	309,700	0	309,700	2,004,629	107,000	2,111,629
1973	3,078,722	n/a	3,078,722	290,000	0	290,000	5,148,026	58,000	5,206,026
1974	2,167,703	n/a	2,167,703	155,400	0	155,400	3,172,943	124,000	3,296,943
1975	1,541,632	n/a	1,541,632	313,100	0	313,100	2,859,739	414,488	3,274,227
1976	1,862,579	n/a	1,862,579	411,665	0	411,665	3,180,237	391,561	3,571,798
1977	1,312,028	n/a	1,312,028	315,804	0	315,804	2,396,756	941,532	3,338,288
1978	1,932,820	n/a	1,932,820	442,742	0	442,742	3,383,606	859,358	4,242,964
1979	2,589,456	n/a	2,589,456	384,030	0	384,030	4,069,020	613,250	4,682,270
1980	2,630,105	n/a	2,630,105	645,929	0	645,929	5,202,443	1,486,357	6,688,800
1981	1,981,170	n/a	1,981,170	331,539	0	331,539	3,729,104	175,515	3,904,619
1982	2,525,414	n/a	2,525,414	1,047,599	0	1,047,599	5,034,698	166,366	5,201,064
1983	2,594,612	n/a	2,594,612	1,872,031	0	1,872,031	6,491,106	346,915	6,838,021
1984	3,111,383	n/a	3,111,383	3,360,350	17,755	3,378,105	9,035,283	640,616	9,675,899
1985	1,824,823	n/a	1,824,823	3,145,229	8,000	3,153,229	8,272,011	467,813	8,739,824
1986	2,221,979	n/a	2,221,979	379,109	0	379,109	7,254,483	1,010,011	8,264,494
1987	1,833,149	n/a	1,833,149	348,660	18,000	366,660	5,646,944	1,043,535	6,690,479
1988	2,156,141	n/a	2,156,141	304,630	0	304,630	6,163,468	2,105,591	8,269,059
1989	2,343,585	n/a	2,343,585	2,376,788	16,038	2,392,826	7,655,294	1,228,408	8,883,702
1990	1,600,059	n/a	1,600,059	1,063,891	24,948	1,088,839	6,716,402	851,478	7,567,880
1991	1,974,923	n/a	1,974,923	3,743,834	38,314	3,782,148	9,077,766	1,047,038	10,124,804
1992	1,689,015	n/a	1,689,015	757,895	0	757,895	7,281,183	1,514,000	8,795,183
1993	1,680,258	n/a	1,680,258	575,062	0	575,062	5,511,171	1,150,177	6,661,348
1994	2,220,595	n/a	2,220,595	752,485	0	752,485	5,810,455	1,351,175	7,161,630
1995	1,878,479	n/a	1,878,479	504,496	0	504,496	5,648,900	1,510,410	7,159,310
1996	1,848,709	n/a	1,848,709	632,081	0	632,081	5,389,729	634,319	6,024,048
1997	1,864,006	n/a	1,864,006	281,813	0	281,813	5,448,866	1,141,469	6,590,335
1998	1,647,000	n/a	1,647,000	313,449	0	313,449	5,126,377	855,595	5,981,972
Subtotal	58,674,554	n/a	58,674,554	25,524,736	123,055	25,647,791	152,432,929	22,285,977	174,718,906